OLD-GROWTH FOREST ASSOCIATIONS IN THE NORTHERN RANGE OF REDWOOD

TOM MAHONY

DECEMBER, 1999

TABLE OF CONTENTS

ABSTRACT

Old-growth redwood (*Sequoia sempervirens*) forests occurring in northwestern California and southwestern Oregon were classified and described using data from 216 systematically placed plots. Data were collected from Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, northern Redwood National Park, and the Siskiyou National Forest. Plot data were analyzed using TWINSPAN and polar ordination. Six associations within the redwood series were classified: *Sequoia sempervirens/Polystichum munitum* (SESE/POMU), *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum* (SESE-PSME/RHMA), *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum* (SESE-TSHE/VAOV), *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* (SESE-TSHE/POMU), *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* (SESE-TSHE/RUSP), and *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* (SESE-ALRU/RUSP).

Discriminant analysis was used to assess the relationships between abiotic site variables and classified floristic associations. Elevation and coastal proximity explained 81.1% of the variation among associations. Aspect and topographic position explained 14.2% of the remaining variation. Moisture was the primary environmental variable controlling the distribution of classified forest associations.

ACKNOWLEDGEMENTS

This thesis is the product of many different people. I thank my major professor Dr. John Stuart for his advice and guidance through every stage of the process, and for sharing his redwood expertise. I'm grateful to Dr. John Sawyer for his interest in this project, and for sharing his encyclopedic knowledge of vegetation classification. Thanks to Dr. Larry Fox for his humor and review of the manuscript. I acknowledge Stephen Underwood and the Vegetation Management Staff at Redwood National and State Parks for providing logistical and technical support throughout this project. Thanks to Jim Belsher for his botanical skills, and for slogging through 5000 hectares of old-growth with me. I thank my parents and family for their love and continued support of my interest in nature. I thank the evening glass at Camel for keeping me sane during this process. I wish to acknowledge the beauty and power of old-growth redwood forests, and thank those who study and preserve these incredible systems. Most of all, I thank Rebecca Shaw for her love, support, and computer expertise.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Redwood

Redwood (*Sequoia sempervirens)* forests are endemic to coastal margins and mesic inland sites from central California to southern Oregon. Along this broad latitudinal gradient, redwood is limited to a narrow belt ten to fifty kilometers wide (Roy 1966, Fox 1989). Precipitation, temperature, and geology change from south to north in the redwood range. Consequently, redwood and it's associates vary in composition from the warmer, drier south, to the cooler, wetter north. Northern redwood forests represent the southern extension of Pacific Northwest forests, containing characteristic species such as *Tsuga heterophylla*, *Picea sitchensis, Thuja plicata*, *Abies grandis*, and *Cupressus lawsoniana*. More southerly redwood stands lack Pacific Northwest conifers, and hardwoods, such as *Lithocarpus densiflorus* and *Arbutus menziesii*, gain importance (Zinke 1977). *Pseudotsuga menziesii* is found throughout most of redwood's range (Roy 1966, McBride and Jacobs 1977).

The extreme northern range of redwood has not been adequately classified and described. Vast tracts of old-growth in Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, and northern sections of Redwood National Park have been virtually ignored in the redwood literature. The difficult access, steep terrain, and huge volume of course woody debris characterizing interior portions of these parks may explain the dearth of botanical information in the region. As a result of this relative isolation, these parks contain some of the most primeval and undisturbed old-growth redwood vegetation in existence.

Southwestern Siskiyou National Forest contains a patchy network of old-growth representing the northernmost natural redwood stands. Since they exist at the terminus of the redwood range, these stands are ecologically significant. They may give insight into processes affecting other parts of the range, including gradients in soil moisture and temperature that affect species composition and stand dynamics. In addition, these northernmost stands may reveal reasons for redwood's abrupt termination at it's northern ecotone, as well as indicate range expansion or contraction (Zinke 1977). The latter is particularly significant in light of projected anthropogenic climate change.

Vegetation Classification

Vegetation classification and description is a logical first step towards improved understanding of redwood ecosystems. Classification simplifies highly complex ecosystems into a manageable number of components and can "bring order out of apparent chaos" (Sawyer and Keeler-Wolf 1995). Classification reduces heterogeneous landscapes into homogeneous units observable in the field which can help describe and predict ecosystem processes. Although classification puts artificial boundaries on inherently continuous phenomena, (Gauch 1982, Sawyer and Keeler-Wolf 1995), resultant groupings can facilitate knowledge, communication, and management of vegetation. These fundamental landscape units, though often coarse and broad in scope, can serve as a framework upon which increasingly finer scale data can be gathered and understood. These data can, in turn, be used by managers and scientists interested in preserving and perpetuating ecosystems. Without this baseline knowledge, successful ecosystem management is unlikely.

Classifications of vegetation are rendered more powerful when floristic associations are linked to physical factors, such as slope, aspect, and elevation. When close correlation exists between biological and physical variables, managers and scientists can use variables, such as those derived from topographic maps, to predict floristic and other biological characteristics of an area without field sampling every site. Though exact correlations are rare in vegetation ecology, definite trends in biophysical relations provided by vegetation classification can greatly reduce the complexity of nature into a few measurable variables that can assist in the ultimate goal of ecology-- prediction. Even if a classification yields weak predictions, it can serve as a framework for further, more detailed or intensive studies which provide greater predictive power.

Vegetation can be classified in different ways depending on the purpose and scope of the classification: functional units used in resource management, such as timber type; vegetation related to landscape units, ecological units, or animal habitats; units emphasizing vegetation structure, floristic assemblages, or units visible on aerial photographs (Sawyer and Keeler-Wolf 1995) . The scale of a classification will reflect the level of detail and purpose of the classification. A vegetation classification of North America, for example, will have a very different resolution than a vegetation classification of a small state park.

Classification scale is represented by hierarchical levels (Table 1). The formation is the highest level, relating broad vegetation units to major differences in environment and physiognomy, such as closed forest vs. woodland. Taxonomic criteria define the classified vegetation units beneath the formation level. The series and subseries represent the dominant life form or combination of life forms, respectively. The association, the lowest unit in the hierarchy, is identified in combination with the series as the dominant life form in subordinate vegetation layers (Sawyer and Keeler-Wolf 1995).

Applying classification techniques to old-growth redwood forests can be particularly informative, because natural processes, such as stand dynamics, can be studied in an environment generally free of human alteration. This knowledge can be useful for managing old-growth forests, or for managing second-growth forests to achieve old-growth characteristics. Within Redwood National and State Parks, both of these management objectives are mandated (Redwood National and State Parks 1998). Old-growth forests within the parks must be perpetuated. Therefore, dynamics operating in old-growth stands must be understood in order to apply management techniques, such as prescribed burning. In addition, within the parks, vast tracts of second-growth redwood must be actively managed in order to achieve old-growth characteristics quicker than what would occur naturally. The resultant old-growth forest would provide suitable habitat for those species requiring old-growth forest vegetation. Management of these forests would be incomplete without a thorough reconnaissance-- a cataloging of flora, habitats, and other ecological characteristics encompassing the region. After intensive, systematic field

Table 1. Hierarchical Levels Used in Vegetation Classification (Sawyer and Keeler-Wolf 1995).

Hierarchical Level	Scale	Example
Formation	community physiognomy	closed forest vs. woodland
Series	dominant species in the overstory	*Sequoia sempervirens*
Sub-Series	dominant set of species in the overstory	*Sequoia sempervirens-Tsuga heterophylla*
Association	dominant species or set of species in the overstory and subordinate vegetation layers	*Sequoia sempervirens-Tsuga heterophylla/ Vaccinium ovatum*

sampling and data analysis, vegetation classification can help meet these management objectives.

Redwood Classifications

Classifications have been done in disparate parts of the redwood range (Becking, 1967, Becking 1971, Dyrness et al. 1972, Atzet and Wheeler 1984, Lenihan 1986, Matthews 1986, Borchert et al. 1988, Fox 1989). However, with the exception of limited sampling by Dyrness et al. (1972), Atzet and Wheeler (1984), and Fox (1989), none have encompassed the extreme northern portion of redwood's distribution. Lenihan (1986) identified three old-growth redwood associations occurring along a moisture gradient in the Little Lost Man Creek Research Natural Area in Redwood National Park, California: *Sequoia sempervirens*/*Blechnum spicant*, *Sequoia sempervirens*/*Berberis nervosa*, and *Sequoia sempervirens*/*Arbutus menziesii*. He considered the associations as moist, mesic, and xeric habitats, respectively. Matthews (1986) described four series, five associations, and one phase in the Bull Creek watershed, Humboldt Redwoods State Park, California: *Sequoia sempervirens*/*Oxalis oregana*, *Sequoia sempervirens-Pseudotsuga menziesii*/*Gaultheria shallon*, *Sequoia sempervirens-Pseudotsuga menziesii*/*Vaccinium ovatum*, *Sequoia sempervirens-Pseudotsuga menziesii*/*Arbutus menziesii*, and *Pseudotsuga menziesii*/*Lithocarpus densiflorus-Arbutus menziesii*. He suggested these associations were arranged along a complex environmental gradient controlled primarily by soil moisture. Becking

(1967) classified redwood vegetation into alliances (roughly equal to series): the Redwood-oxalis alliance (*Sequoia sempervirens-Oxalis oregana*) and Redwood-swordfern alliance (*Sequoia sempervirens-Polystichum munitum*). He indicated that the moist Redwood-oxalis alliance occurred on lower slopes and alluvial flats, and the drier Redwood-swordfern alliance was generally found on middle and upper slopes and ridges. Borchert et al. (1988) classified redwood in the southern part of the range in southern Monterey County, California using the USDA Forest Service's ecological type classification system. They devised six ecological types using biophysical factors: *Sequoia sempervirens*/*Pteridium aquilinum-Woodwardia fimbriata*//Streamsides, *Sequoia sempervirens*/*Polystichum munitum-Trillium ovatum*//Gamboa-sur, *Sequoia sempervirens*//Gamboa-Sur, *Sequoia sempervirens*/*Marah fabaceus-Vicia angustifolia*//Gamboa-Sur, *Sequoia sempervirens-Acer macrophyllum*/*Polypodium californicum*//Gamboa, *Sequoia sempervirens-Lithocarpus densiflorus*/*Carex globosa- Iris douglasiana*//Gamboa. Becking (1971) sampled 26 plots in Monterey County, California, which he placed in the Redwood-tan oak-coulter pine association (*Sequoia sempervirens-Lithocarpus densiflorus-Pinus coulteri*) and the Redwood-tan oak-sorrel association (*Sequoia sempervirens-Lithocarpus densiflorus-Oxalis oregana*). He suggested that the redwood forest distribution in the area was primarily a result of soil moisture, with the former association occurring on drier sites and the latter on moister sites. Fox (1989) presented a classification of the entire range of redwood for use by the California Department of Forestry in wildland resources management. His classification was based on species composition in the overstory as well as seral stage, resulting in the following types: old-growth redwood, second-growth redwood/redwood dominant, second-growth redwood/hardwood dominant, second-growth redwood/Douglas-fir dominant, and plantation.

Purpose

The diversity of associations described in different parts of the range allude to vast geographic variations in biological and physical components of old-growth redwood forests. These differences underscore the importance of classifying the entire range of redwood in order to achieve a complete understanding of the variation found in redwood forests. With this knowledge in hand, managers and scientists will have a solid foundation upon which to build a successful strategy of old-growth redwood forest preservation in their respective management areas.

The primary purpose of this study was to classify and describe the northern range of old-growth redwood, including areas in northern Redwood National Park, Del Norte Coast Redwoods and Jedediah Smith Redwoods State Parks in northwestern California, and the northernmost natural redwood stands in Siskiyou National Forest in southwestern Oregon. This approach is unique in that it investigates redwood's northern range, rather than focusing on an arbitrary management unit. A second major goal of this study was to relate floristic associations to physical factors such as slope, aspect, topographic position, elevation, and coastal proximity.

STUDY AREA

Location

The northern range of redwood, as defined in this study, includes Jedediah Smith Redwoods State Park (JSRSP), Del Norte Coast Redwoods State Park (DNCRSP), the northern section of Redwood National Park (RNP), all located in northern California, and portions of Siskiyou National Forest (SNF) located in southwestern Oregon. The area extends from 41°47'N to 42°10'N, and 124°4'W to 124°12'W. The following USGS topographic quadrangles (7.5' series) provide coverage of the study area: Requa, Childs Hill, Sister Rocks, Crescent City, Hiouchi, Mt. Emily, Fourth of July Creek, and Bosley Butte.

JSRSP, the most northerly of the California State Parks, is located in Del Norte County, California (Figure 1). The campground, park headquarters, and northern park boundary are located 16.6 km northeast of Crescent City, and are accessed by U.S. 199. The park's southern section is accessed by Howland Hill Road. JSRSP consists of 3350 ha of old-growth redwood. Most locations in the park are only accessible by cross-country travel. The Boy Scout Tree trail, Bald Hills trail, and Mill Creek trail provide limited access to the SW, SE, and central sections of the park, respectively.

DNCRSP is located in Del Norte County, California, approximately 5 km south of Crescent City (Figure 2). U.S. 101 provides primary access to the park.

Figure 1. Jedediah Smith Redwoods State Park and Redwood National Park Sections of the Study Area.

Figure 2. Del Norte Coast Redwoods State Park Section of the Study Area.

It consists of 975 ha of old-growth redwood. The Coastal trail and Damnation Creek trail provide limited access to the park.

The portion of RNP in the study area is located adjacent to and south of JSRSP, and is only accessible by Mill Creek Horse Trail or cross-country travel. It consists of 306 ha of old-growth redwood (Figure 1).

The portion of SNF in the study area is located in the Siskiyou Mountains, Curry County, Oregon and administered by the Chetco Ranger District. The nearest community is Brookings, Oregon, 11.3 km north of the California border (Figure 3). U.S. 101 provides primary access to the area. Four stands of old-growth redwood were sampled, most accessed only by Forest Service roads and cross-country travel. The southernmost stand sampled in SNF is located near Peavine Ridge, at 42°0'N, 124°9'W (N1/2, Section 17, T. 41 S., R. 12 W., Willamette meridian), and consists of approximately 130 ha of old-growth. The easternmost stand sampled in SNF is located in Wheeler Creek Research Natural Area at 42°5'N, 124°7'W (Sections 15,16,21, and 22, T. 40 S., R. 12 W., Willamette meridian), containing approximately 135 ha of old-growth. Northwest of the natural area is the westernmost stand sampled, adjacent to Alfred A. Loeb State Park at 42°7'N, 124°12'W (NW1/4, Section 13, T. 40 S., R. 13 W., Willamette meridian), containing approximately 25 ha of old-growth. Good access to this stand is provided by the Redwood Nature Trail. The northernmost stand sampled is located near Snaketooth Butte, at 42°9'N, 124°8'W (NW 1/4, Section 28, T. 39 S., R. 12 W., Willamette meridian), containing approximately 20 ha of old-growth.

Figure 3. Siskiyou National Forest Section of the Study Area.

Topography

The study area is topographically diverse, with elevations ranging from sea level to over 490 m. DNCRSP contains the steepest terrain in the study area, rising from sea level to a 365 m coastal ridge within 700 horizontal meters, yielding gradients of > 50%. JSRSP and RNP are topographically variable, with elongated north-south and east-west ridges, as well as broad alluvial terraces and benches adjacent to the Smith River and Mill Creek. Elevations range from 60 m in the western sections of JSRSP to over 395 m in the southeast corner of the park. Numerous perennial drainages dissect both parks.

The four old-growth stands sampled in SNF are highly diverse, with elevations ranging from 25 m along the Chetco River in Alfred A. Loeb State Park to 490 m in Wheeler Creek Research Natural Area. The Chetco River, Winchuck River, Wheeler Creek and Moser Creek, as well as additional perennial drainages, drain this section of the study area.

Geology

Northwestern California and southwestern Oregon have undergone convergent tectonic processes for most of the Cenozoic era (Bachman et al. 1984). The study area is predominantly underlain by rocks of the Franciscan Formation, a subduction complex consisting of accreted fragments of oceanic crust and forearc sediments. Franciscan rocks are predominantly immature turbidites, with minor amounts of pelagic limestone, greenstone, plutonic rocks, and blueschist facies metamorphic rock (Aalto and Harper 1989). Immediately east of the study area, the Franciscan Formation gives way to the Josephine ophiolite, resulting in a major shift in vegetation from redwood to Douglas-fir (Zinke 1977, Aalto and Harper 1989).

Soils

Soils in the JSRSP, DNCRSP, and RNP portions of the study area were mapped as predominantly Melbourne and Empire series by the California State Cooperative Soil-Vegetation Survey (Smith et al. 1977, Delapp et al. 1978). Empire series soils are most abundant in and around the Clarks Creek drainage in northwestern JSRSP. Unclassified alluvial terrace soils dominate much of the Smith River and Mill Creek floodplains. Melbourne series soils dominate the remainder of this part of the study area. General characteristics of these soils are listed in Table 2.

Climate

California's north coast has a Mediterranean climate, with moderate temperatures, wet winters, and dry summers (Table 3). Rainfall is virtually absent during the summer months, with

90% of the yearly precipitation falling between October and April. Winter precipitation occurs primarily from cyclonic storms moving eastward from

Table 2. General Characteristics of Soil Series (from Smith et al. 1977, Delapp et al. 1978).

Soil Series	Empire	Melbourne
Depth Range (cm)	102-178	114-203
Color of Surface/Subsoil	brown/yellowish brown	very dark brown/light brown and very pale brown
Texture of Surface/Subsoil	loam/clay loam	heavy loam/clay loam and gravely clay loam
Reaction of Surface/Subsoil	moderately acid/strongly acid	moderately acid/strongly acid
Parent Material	soft sedimentary rock	sandstone and shale
Relief	hilly to very steep	steep to very steep
Permeability	moderate	moderate
General Drainage	well drained	well drained
Erosion Hazard	slight to high	moderate
Timber Production	very high to medium	low to very high

Table 3. Temperature and Precipitation for Crescent City, CA, 1948-1998 (National Weather Service 1998).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean Annual
TEMPERATURE (C)													
Highest	22	22	24	32	30	28	26	29	33	31	26	23	33
Mean Maximum	12	13	13	13	16	18	19	19	19	17	15	14	16
Mean Temp	10	9	9	10	12	14	14	15	15	13	11	9	12
Mean Minimum	4	5	5	6	7	9	10	10	10	8	6	5	7
Lowest	-6	-3	-2	0	0	3	5	5	2	0	-2	-3	-6
PRECIPITATION (mm)													
Mean	294	220	216	116	80	35	10	20	45	131	223	280	1664

the Pacific Ocean. Sporadic summer thunderstorms contribute small amounts of precipitation to the inland mountains (National Weather Service 1998).

Along the coast, mean temperatures vary less than 5°C between winter and summer. Peak temperatures along the coastal plain occur in September when the Pacific High Pressure system, with its persistent onshore flow, breaks down and is replaced with a more moderate wind regime as inland areas cool down relative to the Pacific Ocean. Freezing temperatures are experienced along the coast from late December into early March, on average, giving the coastal sector a growing season of 300+ days (National Weather Service 1998).

Fog and stratus are the region's outstanding features and greatly influence coastal redwood forests. Coastal waters remain cool year round due to the cold Humboldt Current, with water temperatures near 11°C. Moist air currents moving over the Pacific Ocean, chilled to their dew point, condense into stratus and fog. The stratus/fog layer is heaviest between sunset and sunrise during August and September due to the Pacific High and it's resultant surface and subsidence inversions (Harris 1987).

Redwood's coastal habitat ensures higher humidities and cooler temperatures, resulting in reduced evapotranspiration. The precise role of fog and fog drip, however, is debatable. Roy (1966) considered summer fog more important to redwood forests than actual precipitation. Azvedo and Morgan (1974) measured fog drip on Peavine and Bear River Ridges near Humboldt Redwoods State Park, California. Their data showed a heavy input of fog drip precipitation during summer months. Byers (1953), however, considered fog drip insignificant to redwood forests. He cited reduced evapotranspiration, resulting from reduced sunshine and daytime temperatures, as fog's primary influence on redwood. Freeman (1971) claimed that high relative humidity and reduced insolation from fog were more important than fog drip in reducing water loss in redwood forests. Harris (1987) suggested that stratus/fog supported redwood development, with redwood in turn controlling the environment and subordinate vegetation development. Regardless of the exact mechanism, fog clearly influences the distribution and ecology of most coastal redwood forests.

Crescent City, California is the closest weather station to the study area. Precipitation data (1948-1998) for Crescent City indicated that maximum precipitation fell during December and January, averaging 28.0 cm and 29.4 cm, respectively. The least amount fell during July and August, averaging 1.0 cm and 2.0 cm, respectively. Annual average precipitation was 166.4 cm (National Weather Service 1998). Generally, precipitation increases as one moves from Crescent City, on the coast, eastward toward the mountains. Snow is rare in the study area.

The highest mean temperatures occurred in Crescent City during August and September, at 14.6° C and 14.5° C, respectively, over a 17 year period. The lowest mean temperatures occurred in February and March, at 8.7° C and 9.0° C, respectively, over the same period. Generally, greater temperature extremes occur in the region as one moves inland from the coast.

Vegetation

Regional vegetation of the study area has been classified and described only at coarse scales. The Society of American Foresters Cover Type Classification (Eyre 1980) mapped the study area entirely within the redwood forest cover type at 1:7,500,000 scale. The redwood vegetation type exists in a continuous band from the study area south to the Mattole River in southern Humboldt County, continuing in disjunct patches south to Monterey County. The eastern and northern edge of the study area region was mapped as the Douglas-fir forest cover type.

Redwood grows primarily within the redwood forest cover type, (Roy 1966), but along the eastern edge, may grow in the Pacific Douglas-fir and the Douglas-fir-tanoak-Pacific madrone types. Sawyer et al. (1977) called this the Mixed Evergreen Forest, dominated by *Pseudotsuga menziesii*, *Lithocarpus densiflorus*, and *Arbutus menziesii*. In fire-free and mesic sites within the Mixed Evergreen Forest, *Tsuga heterophylla* occurs as a codominant with *P. menziesii* and *L. densiflorus*. In the lower Mad River drainage in Humboldt County, *T. heterophylla* and *P. menziesii* share dominance with *Abies grandis* and *Thuja plicata*. *Lithocarpus densiflorus* and *Umbellularia californica* are also present, with an understory dominated by *Polystichum munitum* (Sawyer et al. 1977). West of the redwood forest and adjacent to the coast, the Sitka spruce type forms a narrow band of vegetation in the study area region (Roy 1966). Important conifer species on the coastal side of the redwood type include *Abies grandis*, *Tsuga heterophylla*, and *Picea sitchensis*.

Küchler (1977) classified the study area region as the *Pseudotsuga-Sequoia* forest, with *Sequoia sempervirens* and *Pseudotsuga menziesii* listed as dominants. Other characteristic components include: *Alnus rubra, Arbutus menziesii, Cupressus lawsoniana, Cornus nuttallii, Gaultheria shallon, Lithocarpus densiflorus, Myrica californica, Oxalis oregana, Polystichum munitum, Pteridium aquilinum, Quercus garryana, Rhododendron macrophyllum, R. occidentale, Toxicodendron diversilobum, Thuja plicata, Tsuga heterophylla, Umbellularia californica, Vaccinium ovatum, V. parvifolium,* and *Vancouveria planipetala.*

Zinke (1977) described a transect inland from Big Lagoon (41° 11' 10"N), south of the study area. Along the coast, *Picea sitchensis* and *Abies grandis* dominate, with redwood appearing 1.6 km inland. *Picea sitchensis* drops out within 3-4 km of the coast, while *A. grandis* continues inland. At 5 km inland, a *Lithocarpus densiflorus*-hardwood component appears. Redwood remains the dominant species up to 16 km inland. *Pseudotsuga menziesii* becomes the most abundant conifer inland of 16 km, mixed with a hardwood forest of *L. densiflorus, Quercus garryana*, and *Arbutus menziesii*.

Vegetation has been described in the present study area, but hasn't been subjected to rigorous phytosociological classification. Soil-Vegetation maps (Smith et al. 1977, Delapp et al. 1978) of JSRSP indicate overstories dominated by *Sequoia sempervirens*, *Tsuga heterophylla*, and *Picea sitchensis* in the southwestern sector of the park. Northern sections of the park, south of U.S. 199, are dominated by *S. sempervirens*, *T. heterophylla*, and

Pseudotsuga menziesii. Eastern and southeastern sections are dominated by *S. sempervirens* and *P. menziesii*, with occasional *T. heterophylla* and *Lithocarpus densiflorus*. The portion of RNP in the study area, as indicated on Soil-Vegetation maps, is dominated by *S. sempervirens*, with scattered *T. heterophylla*, *Picea sitchensis*, and *Pseudotsuga menziesii*. Western DNCRSP is dominated primarily by *S. sempervirens*, *Picea sitchensis*, *Pseudotsuga menziesii*, and *T. heterophylla*, with occasional *Alnus rubra*. East of U.S. 101, *S. sempervirens*, *P. menziesii*, and *T. heterophylla* dominate.

Whittaker (1960) conducted limited sampling in JSRSP, 8 km from the coast at 120-180 m elevations. He described a canopy dominated by *Sequoia sempervirens* and a subcanopy of *Tsuga heterophylla* in all topographic situations. *Pseudotsuga menziesii*, *Abies grandis,* and *Cupressus lawsoniana* also occur, with *Picea sitchensis* and *Thuja plicata* occupying moister sites. He cited a sparse lower tree stratum of broad leaved species, including *Lithocarpus densiflorus*, *Corylus cornuta*, *Acer circinatum*, and *Umbellularia californica*. The high shrub stratum is highly developed and dominated by *Vaccinium ovatum* and *V. parvifolium*, particularly on south-facing slopes. Additional undergrowth plants include *Gaultheria shallon, Rhododendron macrophyllum, Oxalis oregana, Polystichum munitum, Blechnum spicant, Viola sempervirens, Galium triflorum, Trillium ovatum, Disporum smithii, Whipplea modesta,* and, in ravines, *Rubus spectabilis, Rhododendron occidentale,* and *Adiantum aleuticum*.

Dyrness et al. (1972) sampled in Wheeler Creek Research Natural Area in SNF in southwestern Oregon. Their limited sampling revealed overstories dominated by *Sequoia sempervirens*, *Pseudotsuga menziesii,* and *Lithocarpus densiflorus.* In mesic lower slopes and ravines, *Acer macrophyllum*, *Umbellularia californica*, and *Alnus rubra* are common. *Tsuga heterophylla* occurs sporadically throughout all but the driest sites. The composition of the overstory and understory in the Natural Area is affected dramatically by site moisture status related to topographic position. The driest sites in the tract, the upper slopes and ridges, are composed of a *Sequoia sempervirens-Pseudotsuga menziesii* canopy, a lower tree stratum of *Lithocarpus densiflorus*, and a dense understory of *Rhododendron macrophyllum* and *Vaccinium ovatum*. Only three other vascular plant species are present and contribute negligible coverage. Mid slope stands, more representative of the site, are similar in composition but have a scattering of seven to fourteen additional plant species in the understory. In mesic sites, *R. macrophyllum* and *V. ovatum* drop out, and herbs, such as *Polystichum munitum*, dominate. Riparian sites are dominated by *Cornus nuttallii*, *Rubus spectabilis*, *Acer circinatum*, *Stachys rigida*, *Carex* sp., *Athyrium filix-femina*, *Blechnum spicant*, and *Asarum caudatum*.

Atzet and Wheeler (1984) classified redwood stands in the Chetco Ranger District in SNF based on potential natural vegetation. They classified these stands as the tanoak-coast redwood series from six field plots. Overstories are dominated by *Pseudotsuga menziesii* and *Sequoia sempervirens*. *Lithocarpus densiflorus* dominates the tree understory, followed by

S. sempervirens, *Tsuga heterophylla*, *Umbellularia californica*, and *P. menziesii*. *Lithocarpus densiflorus* is considered the “climax” dominant based on regeneration patterns in the absence of disturbance. The shrub/herb layer is dominated by *Vaccinium ovatum*, followed by *Polystichum munitum*, *Rhododendron macrophyllum*, *Gaultheria shallon*, and *V. parvifolium*. The association is usually found on metasedimentary parent materials in concavities on northerly exposures.

MATERIALS AND METHODS

Sampling

Three distinct areas were sampled: old-growth redwood in RNP, JSRSP, and DNCRSP, old-growth redwood in SNF, and riparian vegetation in JSRSP. As a result of differences in size and shape of vegetation polygons for each area, as well as availability of vegetation maps and aerial photographs, a slightly different sampling design was used for each area. Each scheme, however, was based on a similar unbiased, systematic sampling protocol.

For RNP, JSRSP, and DNCRSP, 1:12000 color infrared stereo aerial photography was used to delineate old-growth redwood polygons that were structurally and morphologically homogeneous. These units were mapped on mylar overlays and subsequently onto 1:24000 USGS topographic quadrangles. Total polygon area was determined using a digital planimeter. Two hundred plots were stratified based on three elevation classes (0-105 m, 106-215 m, and > 215 m), and placed onto topographic quadrangles in a systematic grid 485 meters apart (total area/number of plots).

Aerial photographs were unavailable for redwood units in SNF. Therefore, old-growth polygons were identified on maps obtained from the USDA Forest Service GIS database, and transferred to 1:24000 USGS topographic quadrangles. Polygons were small compared to RNSP, and therefore a reduced sampling interval was required. The four largest and most accessible polygons were selected for sampling, and polygon area was determined with a digital planimeter. Five plots were placed in each polygon via a systematic sampling grid, with plot spacing determined by polygon area/number of plots.

Riparian vegetation within JSRSP was sampled separately to best characterize this unique and diverse vegetation. Riparian corridors were difficult to map from 1:12000 aerial photographs due to photo scale and overstory canopy. Therefore, to best characterize riparian vegetation within JSRSP, perennial stream length was measured from topographic quadrangles, and total stream length (22,350 m) was divided by plot number (15) to determine spacing. Fifteen sample plots were systematically placed approximately 1500 m apart along Cedar Creek, Mill Creek, Clarks Creek, and several other unnamed perennial drainages within park boundaries. Plots were roughly circular, extending from the stream's edge to an upslope position. Plant cover was estimated out to half of the stream width.

Sampling, conducted from May to July 1997 and May 1998, was restricted to old-growth vegetation. Of 235 plots slated for sampling, 216 were eventually field checked. The remainder were removed from the scheme due to difficult or dangerous access, or the realization, once in the field, that the sample point was not located in old-growth forest. Plot centers were located using pacing, 1:24000 USGS topographic quadrangles, compass, and pocket altimeter. Circular 0.05 ha (500 m^2) plots were thoroughly searched and all vascular plant species identified and recorded with an ocular cover estimate using a modified Braun-Blanquet cover abundance scale (Table 4). Tree species were tallied

Table 4. Cover Abundance Scale Used in Ocular Cover Estimates and Midpoint Used in TWINSPAN Analysis

Cover Scale		
Cover Class	Cover Range	Midpoint
1	.001 - .01%	.006%
2	.01 - .1%	.06%
3	.1 - 1%	.6%
4	1 - 5%	3%
5	5 - 25%	15%
6	25 - 50%	37.5%
7	50 - 75%	62.5%
8	75 - 100%	87.5%

based on stem density in three height classes: 0-3 m, 3-10 m, and >10 m. Basal area, taken from plot center, was estimated for all canopy species. Elevation was determined with a pocket altimeter and topographic map. Slope angle was recorded in percent using a clinometer. Aspect was assessed with a hand compass. Distance from the ocean was estimated using a topographic map. Topographic position was also noted, along with any comments about the stand, such as evidence of fire or disturbance.

Data Analysis

The study classified old-growth redwood vegetation floristically using the Series-Association format, similar to that used by the California Native Plant Society in the Manual of California Vegetation (Sawyer and Keeler-Wolf 1995). This system can crosswalk with other classifications already in use: UNESCO (Muller-Dombois and Ellenberg 1974), and USDA Forest Service (ECOMAP 1993) (Sawyer and Keeler-Wolf 1995). Classification names were based on a combination of dominance and indicator species.

To best characterize the study area's vegetation, field data were analyzed using multivariate analysis. Two-Way Indicator Species Analysis (TWINSPAN), a polythetic, divisive method, was used to simultaneously classify species and samples. TWINSPAN has been widely used in the redwood classification literature (Lenihan 1986, Matthews 1986, Borchert et al. 1988) and has achieved useful results.

TWINSPAN cannot analyze quantitative data directly, but uses “pseudospecies” to make semi-quantitative analysis based on user specified “cut levels”. Pseudospecies cut levels allow the program to retain quantitative information relative to cover abundance scales such as that developed by Braun-Blanquet (Hill 1979). TWINSPAN works by constructing an ordered two-way table based on differential species (species with clear ecological preferences). The program seeks to divide samples into groups by repeated dichotomization in three basic steps. First, samples are ordinated to reveal a direction of data variation. This is based on reciprocal averaging and is know as the “primary ordination”. The ordination is dichotomized by splitting the primary ordination in half, and species preferential to either side of the initial split are identified. Second, a “refined ordination” is constructed from the primary ordination and based on differential species. Finally the “indicator ordination” is constructed based on the most highly preferential species (Hill 1979). The final result is a two-way table grouping species and plots into entities that have more similarity within, rather than between, groups.

Before analysis in TWINSPAN, field data were entered into a spreadsheet. For all non-riparian plots, species occurring in <5% of plots were eliminated from the analysis. The rationale for this was twofold: (1) rare species occurrences are more stochastic than indicative of ecological conditions, and (2) rare species affect multivariate analysis very little because they contain so little of the overall information and variation in the dataset (Gauch 1982). After initial data editing, 201 non-riparian plots were analyzed in TWINSPAN with cut levels of 0.6, 3.0 15.0, 37.5, 62.5, and 87.5. The 15.0 and 37.5 cut levels were weighted to emphasize dominance (Stuart et al. 1996). After initial TWINSPAN analysis, 10 plots were deleted from the main analysis due to their status as outliers. According to Gauch (1982), outliers can obscure the central tendency of the distribution and should be removed.

Riparian plots were analyzed separately, since they obviously differed floristically and structurally, and contained more small, herbaceous species that may have been overlooked in the main analysis. The 15 riparian plots were merged with 54 plots contained on the right side of the primary TWINSPAN division. These 54 plots, based on species literature, physiographic data, and field observations, were the most mesic. The analysis intended to determine if riparian plots would differentiate from the mesic, non-riparian plots. The 69 plots were analyzed after eliminating species occurring in less than 3% of plots. The reduced elimination of rare species (3% as opposed to 5% in the main analysis) allowed for substantially increased plant diversity in riparian plots. These plots were analyzed using the same TWINSPAN cut levels, except dominance was not emphasized due to increased herbaceous biodiversity in riparian assemblages.

TWINSPAN groupings were analyzed using a polar (Bray-Curtis) ordination, to further analyze and refine the TWINSPAN output. Polar ordination attempts to find major gradients in community structure using three basic steps. First, a samples-by-species distance (dissimilarity) matrix is calculated to determine similarity and difference among samples. Second, samples are searched for the most widely separated samples in the distance matrix. These markedly different samples serve as endpoints of the ordination axis, defining direction of community variation. Finally, ordination values are computed for each sample. Samples will fall nearest the endpoint they are most similar to. Samples dissimilar to both endpoints will fall near the center of the ordination axis and samples of similar species composition will cluster together (Gauch 1982). Polar ordination is generally simple and robust. It's main drawback is that different endpoints chosen for the ordination axis can yield different results (Gauch et al. 1977).

Species richness was determined by randomly selecting 5 plots from each association and calculating the mean number of species (Stuart et al. 1996). In addition, stem density per hectare in three height classes and canopy species basal area was averaged for each association.

Discriminant Analysis

A discriminant analysis was performed in NCSS 2000 (Hintze 1998) to relate floristic associations with abiotic site characteristics. Discriminant analysis is a statistical technique assessing differences between two or more groups and a set of discriminating variables (Klecka 1980). Discriminant functions are derived to analyze group differences by giving a particular function's influence on total group separation. The eigenvalue (expressed in individual percentages relative to total percent) indicates how much discriminatory power each function has (Klecka 1980). Standardized canonical coefficients are used to indicate the influence of each variable on each discriminant function. The higher the number (regardless of sign), the greater that variable's contribution. The coefficients are standardized (equal standard deviations) to explain the relative, rather than absolute contribution of each variable (Klecka 1980).

Elevation, slope angle, distance to the ocean, and a Moisture Equivalency Index (MEI) were used as physiographic variables in the discriminant analysis to see which discriminated among the floristic associations most effectively. The MEI was adapted from Sawyer and Thornburgh (1974) and Matthews (1986). It incorporates topographic position and aspect, two variables important to soil moisture. A lower index number assumes greater soil moisture available to plants (Table 5).

Table 5. Moisture Equivalency Index, (Adapted From Sawyer and Thornburgh 1974, and Matthews 1986).

Index Number	Topographic Position	Aspect
1	Seeps	N/A
2	Alluvial Terrace	N/A
3	Lower Slope	NNE, NE
4	Lower Slope	N, ENE
5	Lower Slope	NNW, E
	Middle Slope	NNE, NE
6	Lower Slope	NW, ESE
	Middle Slope	N, ENE
7	Lower Slope	WNW, SE
	Middle Slope	NNW, E
	Upper Slope	NNE, NE
8	Lower Slope	W, SSE
	Middle Slope	NW, ESE
	Upper Slope	N, ENE
9	Lower Slope	WSW, S
	Middle Slope	WNW, SE
	Upper Slope	NNW,E
10	Lower Slope	SW, SSW
	Middle Slope	W, SSE
	Upper Slope	NW, ESE
11	Middle Slope	WSW, S
	Upper Slope	WNW, SE
	Ridge	NNE-ENE
12	Middle Slope	SW, SSW
	Upper Slope	W, SSE
	Ridge	NNE-NW
13	Upper Slope	WSW, S
	Ridge	ESE-S
14	Upper Slope	SW, SSW

	Ridge	W-WSW
15	Ridge	S - WSW

RESULTS

TWINSPAN and polar ordination analysis produced six groups that were interpreted as associations (Figure 4). Groups were consistent with vegetation units observed in the field. All associations were in the *Sequoia sempervirens* series; *Pseudotsuga menziesii, Tsuga heterophylla,* and *Alnus rubra* were the sub-series identified by the analysis. The first TWINSPAN division separated groups based on understories dominated by either *Vaccinium ovatum* or *Polystichum munitum*. Within these broad groupings, subsequent TWINSPAN division levels reflected groupings based on other indicator understory species such as *Lithocarpus densiflorus, Rhododendron macrophyllum,* and *Rubus spectablilis*.

Polar ordination was used to further confirm and analyze TWINSPAN groups. The two methods showed good agreement, especially for the initial TWINSPAN break. The ordination separated into two main groups that represented the left and right sides, respectively, of the primary TWINSPAN division (Figure 5). The ordination revealed greater within group homogeneity for the left side plots compared to the right side. Overall, the polar ordination supported the TWINSPAN classification.

The six associations produced by the TWINSPAN and polar ordination analysis were: *Sequoia sempervirens/Polystichum munitum* (SESE/POMU), *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum* (SESE-PSME/RHMA), *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum* (SESE-TSHE/VAOV), *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum*

Figure 4. Dendrogram depicting TWINSPAN classification. Annotation indicates significant classification factors.

Figure 5. Polar Ordination Depicting Primary TWINSPAN Division. A is SESE-PSME/RHMA and SESE-TSHE/VAOV. B is SESE/POMU and SESE-TSHE/POMU

(SESE-TSHE/POMU), *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* (SESE-TSHE/RUSP), and *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* (SESE-ALRU/RUSP).

The *Sequoia sempervirens/Polystichum munitum* Association

The *Sequoia sempervirens/Polystichum munitum* association ranged from 21-369 m elevation, averaging 143 m. Distance from the ocean averaged 6.4 km. Slopes averaged 36 percent, and Moisture Equivalency Index (MEI) scores averaged 7.5. Species richness averaged 19 species (Table 6, Figures 6, 7, and 8).

Total vegetation cover averaged 90 percent. Total overstory cover averaged 76 percent. *Sequoia sempervirens* dominated the canopy with 60 percent cover and 100 percent constancy. *Tsuga heterophylla* was common, and *Pseudotsuga menziesii* appeared occasionally in the canopy. *Abies grandis*, *Cupressus lawsoniana,* and *Umbellularia californica* occurred sporadically, contributing minimal cover. *Lithocarpus densiflorus* was ubiquitous in the subcanopy (Tables 7 and 8, Figure 9).

The 0-3 m tree layer was dominated by *L. densiflorus* with 41 stems/ha, followed by, in decreasing order of abundance, *S. sempervirens*, *T. heterophylla* and *A. grandis*. The 3-10 m layer was dominated by *S. sempervirens* with 33 stems/ha, followed by *L. densiflorus*, *T.*

heterophylla, *P. menziesii*, and *A. grandis*. *Sequoia sempervirens* had the most total stems/ha (164), followed by *T. heterophylla, L. densiflorus, A. grandis*, and *P.*

Table 6. Mean Environmental Characteristics of Associations.

	SESE-PSME/ RHMA	SESE-TSHE/ VAOV	SESE/POMU	SESE-TSHE/ POMU	SESE-TSHE/ RUSP	SESE-ALRU/ RUSP
Elevation (m)	312	161	143	114	67	136
Distance (km)	8.5	7.4	6.4	5.5	6.8	3.6
Slope (%)	42.9	36.2	36.2	34.9	38.0	49.7
MEI (1-15)	9.8	9.0	7.5	7.0	1.3	6.7

Figure 6. *Sequoia sempervirens/Polystichum munitum* Association, Boy Scout Tree Trail, Jedediah Smith Redwoods State Park.

Figure 7. 3-D Scatterplot Depicting Forest Associations in Relation to Elevation, Distance From the Ocean, and Topographic Position/Aspect (MEI).

Figure 8. 3-D Scatterplot Depicting Forest Associations in Relation to Elevation, Distance From the Ocean, and Topographic Position/Aspect (MEI) (Different Perspective).

Table 7. Mean Cover (Percentage) for Species Used in the Analysis by Association.

Species	SESE-PSME/RHMA	SESE-TSHE/VAOV	SESE/POMU	SESE-TSHE/POMU	SESE-TSHE/RUSP	SESE-ALRU/RUSP
Abies grandis	0.00	4.58	1.72	0.94	0.00	3.00
Acer circinatum	0.00	0.00	1.29	0.64	19.00	7.75
Acer macrophyllum	0.00	0.00	0.23	0.00	10.07	3.00
Achlys californica	0.06	0.01	0.04	0.00	0.09	0.00
Adenocaulon bicolor	0.00	0.08	0.02	0.08	0.01	0.00
Adiantum aleuticum	0.00	0.02	0.06	0.01	0.77	0.37
Alnus rubra	0.02	0.30	1.10	0.33	2.57	38.36
Asarum caudatum	0.09	0.10	1.07	0.08	0.20	0.61
Athyrium filix-femina	0.00	0.01	0.09	0.51	1.55	2.28
Berberis nervosa	0.29	1.15	0.17	0.03	0.09	0.00
Blechnum spicant	0.20	2.99	3.75	10.45	9.51	0.25
Boykinia occidentalis	0.00	0.00	0.00	0.08	0.18	0.07
Bromus vulgaris	0.00	0.00	0.00	0.03	0.09	0.06
Cardamine californica	0.12	0.15	0.11	0.00	0.01	0.00
Cardamine oligosperma	0.00	0.00	0.00	0.00	0.17	0.07
Carex deweyana	0.00	0.00	0.00	0.06	0.01	0.13
Carex hendersonii	0.00	0.01	0.00	0.08	0.00	0.00
Carex obnupta	0.00	0.00	0.00	0.01	0.00	0.06
Claytonia sibirica	0.00	0.00	0.01	0.02	0.00	0.16
Clintonia andrewsiana	0.05	0.22	0.05	0.08	0.02	0.00
Corylus cornuta	0.13	0.16	3.19	0.38	13.64	4.35
Cyperus niger	0.00	0.00	0.00	0.00	0.09	0.06
Cystoperis fragilis	0.00	0.00	0.00	0.00	0.01	0.06
Disporum hookeri	0.08	0.20	0.21	0.07	0.01	0.00
Disporum smithii	0.03	0.02	0.11	0.43	0.29	0.02
Dryopteris expansa	0.00	0.04	0.36	1.46	1.05	1.93
Equisetum telmateia	0.00	0.00	0.00	0.01	0.45	0.01
Erechtites glomerata	0.00	0.00	0.00	0.01	0.09	0.19
Erechtites minima	0.00	0.00	0.00	0.00	0.00	0.13
Galium triflorum	0.02	0.07	0.05	0.07	0.03	0.04
Gaultheria shallon	2.44	1.95	4.49	1.02	5.70	9.65
Glyceria elata	0.00	0.00	0.00	0.00	0.09	0.06
Goodyera oblongifolia	0.01	0.03	0.00	0.00	0.00	0.00
Hierochloe occidentalis	0.00	0.19	0.11	0.03	0.01	0.00
Lilium columbianum	0.05	0.03	0.00	0.00	0.00	0.00
Lithocarpus densiflorus	45.24	20.57	15.87	1.32	8.01	3.87
Luzula comosa	0.00	0.00	0.01	0.02	0.09	0.01
Lysichiton americanum	0.00	0.00	0.00	0.00	0.51	0.00
Maianthemum dilatatum	0.00	0.04	1.35	0.54	0.60	0.30

Table 7. Mean Cover, (Percentage) for Species Used in the Analysis (Continued).

Species	SESE-PSME/ RHMA	SESE-TSHE/ VAOV	SESE/POMU	SESE-TSHE/ POMU	SESE-TSHE/ RUSP	SESE-ALRU/ RUSP
Marah oreganus	0.00	0.00	0.01	0.15	0.17	4.84
Melica subulata	0.00	0.02	0.01	0.02	0.01	0.01
Menziesia ferruginea	0.00	0.01	0.06	2.52	3.00	0.00
Mimulus dentatus	0.00	0.00	0.00	0.07	0.02	0.00
Oenanthe sarmentosa	0.00	0.00	0.00	0.00	0.09	0.06
Oxalis oregana	0.68	0.89	13.37	9.05	15.60	15.30
Petasites frigidus	0.00	0.00	0.00	0.00	0.09	0.36
Phalaris arundinacea	0.00	0.00	0.00	0.00	0.09	0.36
Physocarpus capitatus	0.00	0.00	0.00	0.00	0.00	0.31
Picea sitchensis	0.00	0.00	0.28	2.95	5.36	7.56
Pleuropogon refractus	0.00	0.00	0.00	0.01	0.00	0.06
Polypodium glycyrrhiza	0.03	0.00	0.01	0.01	0.00	0.31
Polypodium scouleri	0.00	0.04	0.05	0.09	0.01	0.08
Polystichum munitum	7.02	12.18	55.20	66.63	30.07	23.71
Pseudotsuga menziesii	31.15	17.22	5.38	1.47	0.43	3.06
Pteridium aquilinum	0.16	0.03	0.11	0.03	0.00	0.30
Ranunculus repens	0.00	0.00	0.00	0.00	0.09	0.30
Rhamnus purshiana	0.03	0.08	0.39	0.33	0.95	4.06
Rhododendron macrophyllum	34.71	12.92	3.33	1.17	0.00	0.00
Ribes bracteosum	0.00	0.00	0.00	0.06	1.03	0.00
Rosa gymnocarpa	0.00	0.01	0.06	0.00	0.00	0.00
Rubus discolor	0.00	0.00	0.00	0.00	0.00	0.12
Rubus parviflorus	0.00	0.06	0.05	0.01	0.26	2.65
Rubus spectabilis	0.00	0.01	0.14	5.37	24.60	21.74
Rubus ursinus	0.00	0.00	0.00	0.01	0.09	0.37
Rumex crispus	0.00	0.00	0.00	0.00	0.00	0.36
Sambucus racemosa	0.00	0.01	0.00	0.07	0.51	2.58
Satureja douglasii	0.00	0.00	0.00	0.00	0.86	0.00
Sequoia sempervirens	42.96	36.66	60.35	53.29	22.30	35.75
Stachys ajugoides	0.00	0.00	0.02	0.04	0.10	0.11
Streptopus amplexifolius	0.00	0.00	0.00	0.03	0.17	0.00
Thuja plicata	0.00	0.00	0.05	0.31	2.57	0.00
Tolmiea menziesii	0.00	0.00	0.00	0.06	0.12	1.75
Toxicodendron diversilobum	0.02	0.00	0.04	0.00	0.01	0.30
Trisetum cernuum	0.00	0.03	0.03	0.03	0.00	0.00
Trientalis latifolia	0.01	0.04	0.02	0.01	0.00	0.00
Trillium ovatum	0.53	0.68	0.68	0.33	0.28	0.13

Table 7. Mean Cover, (Percentage) for Species Used in the Analysis (Continued).

Species	SESE-PSME/ RHMA	SESE-TSHE/ VAOV	SESE/POMU	SESE-TSHE/ POMU	SESE-TSHE/ RUSP	SESE-ALRU/ RUSP
Tsuga heterophylla	1.47	40.82	24.25	39.18	20.79	0.00
Umbellularia californica	0.14	0.01	0.82	0.00	2.14	1.51
Vaccinium ovatum	46.91	51.39	16.03	14.40	5.14	2.10
Vaccinium parvifolium	1.10	1.93	2.96	4.46	3.26	0.00
Vancouveria hexandra	0.00	1.78	0.06	0.25	0.34	0.01
Viola glabella	0.00	0.00	0.00	0.00	0.01	0.07
Viola sempervirens	0.21	0.24	0.04	0.10	0.02	0.01
Whipplea modesta	0.00	0.03	0.00	0.01	0.00	0.00

Table 8. Mean Constancy for Species Used in the Analysis. Constancy is the Number of Occurrences a Species has in an Association as a Percentage of Total Plots.

Species	SESE-PSME/ RHMA	SESE-TSHE/ VAOV	SESE/POMU	SESE-TSHE/ POMU	SESE-TSHE/ RUSP	SESE-ALRU/ RUSP
Abies grandis	0	20	16	6	0	20
Acer circinatum	0	0	11	6	71	20
Acer macrophyllum	0	0	2	0	57	20
Achlys californica	26	6	11	0	14	0
Adenocaulon bicolor	4	12	14	10	14	0
Adiantum aleuticum	0	4	16	2	71	30
Alnus rubra	4	2	6	4	29	100
Asarum caudatum	15	10	47	13	71	70
Athyrium filix-femina	0	2	20	58	100	60
Berberis nervosa	41	44	31	6	14	0
Blechnum spicant	26	72	73	96	100	50
Boykinia occidentalis	0	0	2	4	43	20
Bromus vulgaris	0	0	0	4	14	10
Cardamine californica	11	28	22	2	14	0
Cardamine oligosperma	0	0	0	0	29	20
Carex deweyana	0	0	0	2	14	30
Carex hendersonii	0	4	8	4	0	0
Carex obnupta	0	0	0	2	0	10
Claytonia sibirica	4	8	5	8	0	80
Clintonia andrewsiana	15	38	22	10	29	0
Corylus cornuta	7	12	25	4	57	30
Cyperus niger	0	0	0	0	14	10
Cystoperis fragilis	0	0	0	0	14	10
Disporum hookeri	37	54	66	29	14	0
Disporum smithii	22	14	48	67	100	40
Dryopteris expansa	0	14	36	75	86	50
Equisetum telmateia	0	0	0	2	43	10
Erechtites glomerata	4	0	0	0	0	30
Erechtites minima	4	0	0	2	14	40
Galium triflorum	37	54	61	17	57	60
Gaultheria shallon	78	74	80	75	71	80
Glyceria elata	0	0	0	0	14	10
Goodyera oblongifolia	19	18	5	2	0	0
Hierochloe occidentalis	0	26	19	4	14	0
Lilium columbianum	19	8	2	0	0	0
Lithocarpus densiflorus	100	94	95	31	57	30
Luzula comosa	4	4	9	15	14	20
Lysichiton americanum	0	0	0	0	29	0

Table 8. Mean Constancy for Species Used in the Analysis (Continued).

Species	SESE-PSME/ RHMA	SESE-TSHE/ VAOV	SESE/POMU	SESE-TSHE/ POMU	SESE-TSHE/ RUSP	SESE-ALRU/ RUSP
Maianthemum dilatatum	0	10	20	52	43	10
Marah oreganus	0	2	6	21	29	80
Melica subulata	0	4	8	6	14	10
Menziesia ferruginea	0	4	6	69	43	0
Mimulus dentatus	0	0	2	6	29	0
Oenanthe sarmentosa	0	0	0	0	14	10
Oxalis oregana	52	78	98	100	100	30
Petasites frigidus	0	0	0	0	14	20
Phalaris arundinacea	0	0	0	0	14	20
Physocarpus capitatus	0	0	0	0	0	20
Picea sitchensis	0	0	3	19	14	30
Pleuropogon refractus	0	0	0	2	0	10
Polypodium glycyrrhiza	11	2	8	2	0	20
Polypodium scouleri	0	10	23	17	14	50
Polystichum munitum	93	100	100	100	100	100
Pseudotsuga menziesii	100	78	44	13	14	30
Pteridium aquilinum	33	12	8	4	0	10
Ranunculus repens	0	0	0	0	14	10
Rhamnus purshiana	30	34	38	60	57	40
Rhododendron macrophyllum	100	76	41	17	0	0
Ribes bracteosum	0	0	0	2	57	0
Rosa gymnocarpa	4	2	9	0	0	0
Rubus discolor	0	0	0	0	0	20
Rubus parviflorus	0	2	9	2	43	90
Rubus spectabilis	4	4	31	63	100	100
Rubus ursinus	0	0	2	2	14	30
Rumex crispus	0	0	0	0	0	20
Sambucus racemosa	0	2	2	17	29	70
Satureja douglasii	0	0	0	0	29	0
Sequoia sempervirens	96	100	100	98	86	80
Stachys ajugoides	0	0	16	13	43	90
Streptopus amplexifolius	0	0	0	8	29	0
Thuja plicata	0	0	2	2	29	0
Tolmiea menziesii	0	0	0	2	71	60
Toxicodendron diversilobum	4	4	9	0	14	10

Table 8. Mean Constancy for Species Used in the Analysis (Continued).

Species	SESE-PSME/ RHMA	SESE-TSHE/ VAOV	SESE/POMU	SESE-TSHE/ POMU	SESE-TSHE/ RUSP	SESE-ALRU/ RUSP
Trisetum cernuum	4	16	16	4	0	0
Trientalis latifolia	19	20	19	2	0	0
Trillium ovatum	93	98	98	69	86	30
Tsuga heterophylla	22	100	75	88	86	0
Umbellularia californica	19	10	19	0	14	30
Vaccinium ovatum	100	98	97	98	57	70
Vaccinium parvifolium	70	70	73	94	86	0
Vancouveria hexandra	4	26	55	27	57	10
Viola glabella	0	0	0	0	14	20
Viola sempervirens	74	90	61	31	29	10
Whipplea modesta	4	30	8	4	0	0

Figure 9. Mean Cover of Selected Species by Association.

menziesii (Table 9). *Sequoia sempervirens* had the greatest basal area (165 m^2/ha) followed by, in decreasing order of abundance, *T. heterophylla*, *P. menziesii*, and *A. grandis*. Total canopy basal area for this association averaged 192 m^2/ha (Table 10).

Vaccinium ovatum dominated the moderate shrub layer, averaging 16 percent cover and 97 percent constancy. *Gaultheria shallon, Rhododendron macrophyllum*, and *Vaccinium parvifolium* were common but each averaged less than 5 percent cover. *Acer circinatum*, *Berberis nervosa, Corylus cornuta,* and *Rubus spectabilis* occurred sporadically, contributing minimal cover (Tables 7 and 8).

Herbaceous cover and species diversity was moderately high. *Polystichum munitum* dominated, averaging 55 percent cover and 100 percent constancy. *Oxalis oregana* was extremely common. Additional species included *Asarum caudatum, Athyrium filix-femina, Blechnum spicant, Cardamine californica, Clintonia andrewsiana Disporum hookeri, Disporum smithii, Dryopteris expansa, Galium triflorum, Maianthemum dilatatum, Polypodium scouleri, Trillium ovatum, Vancouveria hexandra*, and *Viola sempervirens* (Tables 7 and 8).

The *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum* Association

The *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum* association ranged in elevation from 58-470 m, averaging 312 m. Distance from the ocean

Table 9. Mean Number of Stems Per Hectare in Three Height Classes for Selected Tree Species by Association.

Species	0-3m (#/ha)	3-10m (#/ha)	>10m (#/ha)	Total (#/ha)
SESE-PSME/RHMA				
Sequoia sempervirens	17.0	37.2	66.0	120.2
Pseudotsuga menziesii	1.4	7.4	56.4	65.2
Tsuga heterophylla	2.2	5.2	1.4	8.8
Picea sitchensis	0.0	0.0	0.0	0.0
Abies grandis	0.0	0.0	0.0	0.0
Lithocarpus densiflorus	51.2	77.8	57.0	186.0
Total	71.8	127.6	180.8	380.2
SESE-TSHE/VAOV				
Sequoia sempervirens	13.6	12.8	52.4	78.8
Pseudotsuga menziesii	0.0	2.8	29.2	32.0
Tsuga heterophylla	42.8	28.0	81.6	152.4
Picea sitchensis	0.0	0.0	0.0	0.0
Abies grandis	2.4	1.6	10.4	14.4
Lithocarpus densiflorus	28.8	31.6	32.4	92.8
Total	87.6	76.8	206.0	370.4
SESE/POMU				
Sequoia sempervirens	39.0	33.2	91.6	163.8
Pseudotsuga menziesii	0.0	2.8	11.2	14.0
Tsuga heterophylla	20.4	21.0	48.4	89.8
Picea sitchensis	0.0	0.0	0.0	0.0
Abies grandis	13.4	1.8	5.0	20.2
Lithocarpus densiflorus	41.2	27.8	16.2	85.2
Total	114.0	86.6	172.4	373.0

Table 9. Mean Number of Stems Per Hectare in Three Height Classes for Selected Tree Species by Association (Continued).

Species	0-3m (#/ha)	3-10m (#/ha)	>10m (#/ha)	Total (#/ha)
SESE-TSHE/POMU				
Sequoia sempervirens	17.0	25.0	74.6	116.6
Pseudotsuga menziesii	0.0	0.0	1.2	1.2
Tsuga heterophylla	31.2	36.2	74.2	141.6
Picea sitchensis	1.6	1.6	9.2	12.4
Abies grandis	0.0	0.0	5.0	5.0
Lithocarpus densiflorus	4.2	3.4	1.6	9.2
Total	54.0	66.2	165.8	286.0
SESE-TSHE/RUSP				
Sequoia sempervirens	5.8	8.6	14.2	28.6
Pseudotsuga menziesii	0.0	0.0	3.4	3.4
Tsuga heterophylla	40.0	17.2	37.2	94.4
Picea sitchensis	2.8	0.0	5.8	8.6
Abies grandis	0.0	0.0	0.0	0.0
Lithocarpus densiflorus	20.0	25.8	11.4	57.2
Total	68.6	51.6	72.0	192.2
SESE-ALRU/RUSP				
Sequoia sempervirens	58.0	78.0	74.0	210.0
Pseudotsuga menziesii	2.0	0.0	6.0	8.0
Tsuga heterophylla	0.0	0.0	0.0	0.0
Picea sitchensis	0.0	12.0	12.0	24.0
Abies grandis	0.0	16.0	2.0	18.0
Lithocarpus densiflorus	10.0	4.0	14.0	28.0
Alnus rubra	4.0	58.0	62.0	124.0
Total	74.0	168.0	170.0	412.0

Table 10. Mean Basal Area (m^2/ha) for Canopy Species by Association.

Species	SESE-PSME/ RHMA	SESE-TSHE/ VAOV	SESE/POMU	SESE-TSHE/ POMU	SESE-TSHE/ RUSP	SESE-ALRU/ RUSP
Sequoia sempervirens	86.0	114.0	165.0	170.0	73.0	87.0
Pseudotsuga menziesii	37.0	21.0	10.0	2.0	2.0	7.0
Tsuga heterophylla	0.4	23.0	15.0	23.0	11.0	0.0
Picea sitchensis	0.0	0.0	0.0	4.0	6.0	10.0
Abies grandis	0.0	3.0	1.0	0.2	0.0	3.0
Total Basal Area	123.4	161.0	192.0	199.2	92.0	107.0

averaged 8.5 km. Slopes averaged 43 percent, and MEI scores averaged 9.8. Species richness averaged 13.6 species (Table 6, Figures 7, 8, and 10).

Total vegetation cover averaged 85 percent, and total overstory cover averaged 68 percent. Overstories were dominated by *Sequoia sempervirens* and *Pseudotsuga menziesii*, with mean cover values of 43 and 31 percent, respectively, and mean constancies of 96 and 100 percent, respectively. *Tsuga heterophylla* was occasionally present but contributed minimal cover. *Lithocarpus densiflorus* dominated the sub-canopy (Tables 7 and 8, Figure 9).

The 0-3 m tree layer was dominated by *L. densiflorus*, with 51 stems/ha, followed by, in decreasing order of abundance, *S. sempervirens*, *P. menziesii*, and *T. heterophylla*. The 3-10 m layer was dominated by *L. densiflorus* with 78 stems/ha, followed *by S. sempervirens, P. menziesii*, and *T. heterophylla*. The >10 m layer was dominated by *S. sempervirens* with 66 stems/ha, followed by *L. densiflorus, P. menziesii*, and *T. heterophylla*. *Lithocarpus densiflorus* had the greatest number of stems/ha (186), followed by *S. sempervirens, P. menziesii,* and *T. heterophylla* (Table 9). Basal area was highest for *S. sempervirens*, (86 m^2/ha), followed by, in decreasing order of abundance, *P. menziesii* and *T. heterophylla*. Total canopy tree basal area averaged 123 m^2/ha (Table 10).

The shrub layer was extremely dense. *Vaccinium ovatum* and *Rhododendron macrophyllum* dominated, with mean cover values of 47 and 35 percent, respectively, and mean constancies of 100 and 100 percent, respectively. *Berberis nervosa*, *Gaultheria*

Figure 10. *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum* Association, Redwood Nature Trail, Siskiyou National Forest.

shallon, *Rhamnus purshiana*, and *Vaccinium parvifolium* were common but contributed minimal cover (Tables 7 and 8).

The herb layer was virtually absent. *Polystichum munitum* was the most dominant species in this layer with 7 percent cover and 93 percent constancy. *Disporum hookeri, Galium triflorum, Oxalis oregana, Trillium ovatum,* and *Viola sempervirens* were common but contributed negligible cover. *Achlys californica* and *Pteridium aquilinum* occurred sporadically (Tables 7 and 8).

The *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum* Association

The *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum* association ranged from 40-460 m elevation, averaging 161 m. Distance inland averaged 7.4 km. Slopes averaged 36 percent, and MEI scores averaged 9. Species richness averaged 16.6 species (Table 6, Figures 7, 8, and 11).

Total vegetation cover averaged 88 percent, and total overstory cover averaged 74 percent. *Sequoia sempervirens, Tsuga heterophylla*, and *Pseudotsuga menziesii* dominated the canopy, with mean covers of 37, 41, and 17 percent, respectively, and mean constancies of 100, 100, and 78 percent, respectively. *Abies grandis* appeared occasionally in the canopy. *Lithocarpus densiflorus* was common in the subcanopy (Tables 7 and 8, Figure 9).

Figure 11. *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum* Association, Little Bald Hills Trail, Jedediah Smith Redwoods State Park.

The 0-3 m tree layer was dominated by *T. heterophylla*, averaging 43 stems/ha, followed by, in decreasing order of abundance, *L. densiflorus, S. sempervirens,* and *A. grandis*; *Pseudotsuga menziesii* was absent in this layer. The 3-10 m layer was dominated by *L. densiflorus* with 32 stems/ha, followed by *T. heterophylla, S. sempervirens, P. menziesii*, and *A. grandis*. The >10 m layer was dominated by *T. heterophylla* with 82 stems/ha, followed by *S. sempervirens, L. densiflorus, P. menziesii*, and *A. grandis*. *Tsuga heterophylla* had the greatest total number of stems/ha (152), followed by *L. densiflorus, S. sempervirens, P. menziesii*, and *A. grandis* (Table 9). *Sequoia sempervirens* dominated canopy basal area, averaging 114 m^2/ha, followed by, in decreasing order of abundance, *T. heterophylla, P. menziesii*, and *A. grandis*. Total canopy tree basal area for this association averaged 161 m^2/ha (Table 10).

The shrub layer was dense. *Vaccinium ovatum* dominated, averaging 51 percent cover and 98 percent constancy. *Rhododendron macrophyllum* was common. *Berberis nervosa*, *Gaultheria shallon* and *Vaccinium parvifolium* were common but had minimal cover. *Corylus cornuta* and *Rhamnus purshiana* occurred sporadically (Tables 7 and 8).

The herb layer was dominated by *Polystichum munitum*, averaging 12 percent cover and 100 percent constancy. Other species included *Blechnum spicant, Cardamine californica, Clintonia andrewsiana, Disporum hookeri, Galium triflorum, Hierochloe occidentalis, Oxalis oregana, Trientalis latifolia, Trillium ovatum, Vancouveria hexandra, Viola sempervirens*, and *Whipplea modesta* (Tables 7 and 8).

The *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* Association

The *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* association ranged from 40-274 m elevation, averaging 114 m. Distance inland averaged 5.5 km. Slopes averaged 35 percent, and MEI scores averaged 7. Species richness averaged 15.6 species (Table 6, Figures 7, 8, and 12).

Total vegetation cover averaged 92 percent, and total overstory cover averaged 75 percent. *Sequoia sempervirens* and *Tsuga heterophylla* dominated the canopy, with mean covers of 53 and 39 percent, respectively, and mean constancies of 98 and 88 percent, respectively. *Abies grandis*, *Lithocarpus densiflorus*, *Picea sitchensis* and *Pseudotsuga menziesii* occurred sporadically, contributing minimal cover. *Thuja plicata* appeared occasionally in mesic sites (Tables 7 and 8, Figure 9).

Tsuga heterophylla dominated the 0-3 m tree layer with 31 stems/ha followed by, in decreasing order of abundance, *S. sempervirens, L. densiflorus,* and *Picea sitchensis.* The 3-10 m layer was dominated by *T. heterophylla* with 36 stems/ha, followed by *S. sempervirens, L. densiflorus* and *P. sitchensis*. The >10 m layer was dominated by *S. sempervirens* at 75 stems/ha, followed by *T. heterophylla, P. sitchensis, A. grandis, L. densiflorus,* and *Pseudotsuga menziesii.* *Tsuga heterophylla* had the most total stems/ha, (142), followed by *S. sempervirens, Picea sitchensis, L. densiflorus, A. grandis,* and

Pseudotsuga menziesii (Table 9). *Sequoia sempervirens* dominated basal area (170 m^2/ha) followed by, in decreasing order of abundance, *T. heterophylla*, *Picea sitchensis*,

Figure 12. *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* Association, Boy Scout Tree Trail, Jedediah Smith Redwoods State Park.

Pseudotsuga menziesii, and *A. grandis*. Total canopy basal area for this association averaged 199 m^2/ha (Table 10).

The shrub layer was generally not well developed. *Vaccinium ovatum* was the most abundant shrub, averaging 14 percent cover and 98 percent constancy. *Menziesia ferruginea*, *Rubus spectabilis*, and *Vaccinium parvifolium* were common. *Gaultheria shallon* and *Rhamnus purshiana* were common but contributed minimal cover (Tables 7 and 8).

The herbaceous layer was dense. *Polystichum munitum* dominated, averaging 67 percent cover and 100 percent constancy. *Blechnum spicant* and *Oxalis oregana* were common. Other species included *Athyrium filix-femina*, *Disporum hookeri*, *Disporum smithii*, *Dryopteris expansa*, *Maianthemum dilatatum*, *Marah oreganus*, *Trillium ovatum*, *Vancouveria hexandra*, and *Viola sempervirens* (Tables 7 and 8).

The *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* Association

This association ranged from 37-122 m elevation, averaging 67 m. Distance from the ocean averaged 6.8 km. Slopes averaged 38 percent, and MEI scores averaged 1.3. Species richness averaged 26.8 species (Table 6, Figures 7, 8, and 13).

Total vegetation cover averaged 94 percent, and total overstory cover averaged 55 percent. *Sequoia sempervirens* and *Tsuga heterophylla* were canopy dominants, averaging 22 and 21 percent cover, respectively, and 86 and 86 percent constancy, respectively. *Picea sitchensis* and *Thuja plicata* were occasional to common in mesic

Figure 13. *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* Association, Boy Scout Tree Trail, Jedediah Smith Redwoods State Park.

sites. *Pseudotsuga menziesii* occurred sporadically. *Acer macrophyllum* was common, especially near stream channels. *Lithocarpus densiflorus* was common in the subcanopy. *Alnus rubra* and *Sambucus racemosa* appeared occasionally (Tables 7 and 8, Figure 9). The 0-3 m tree layer was dominated by *T. heterophylla*, averaging 40 stems/ha, followed by, in decreasing order of abundance, *L. densiflorus, S. sempervirens*, and *Picea sitchensis*. The 3-10 m layer was dominated by *L. densiflorus* at 26 stems/ ha, followed by *T. heterophylla* and *S. sempervirens*. The >10 m layer was dominated by *T. heterophylla* at 37 stems/ha, followed by *S. sempervirens, L. densiflorus, P. sitchensis*, and *Pseudotsuga menziesii*. *Tsuga heterophylla* had the most total stems/ha, (94), followed by *L. densiflorus, S. sempervirens, Picea sitchensis*, and *Pseudotsuga menziesii* (Table 9). *Sequoia sempervirens* had the greatest basal area (73 m^2/ha) followed by, in decreasing order of abundance, *T. heterophylla, Picea sitchensis*, and *Pseudotsuga menziesii*. Total canopy basal area for this association averaged 91 m^2/ha (Table 10).

Rubus spectabilis dominated the dense shrub layer, averaging 25 percent cover and 100 percent constancy. *Acer circinatum* and *Corylus cornuta* were abundant in this layer. Other common shrubs included *Gaultheria shallon, Menziesia ferruginea, Rhamnus purshiana, Ribes bracteosum, Rubus parviflorus, Vaccinium ovatum*, and *V. parvifolium* (Tables 7 and 8).

The herbaceous layer was dense and floristically diverse. *Polystichum munitum* dominated with 31 percent cover and 100 percent constancy. *Oxalis oregana* and *Blechnum* *spicant* were abundant. Other species included *Adiantum aleuticum, Asarum caudatum, Athyrium filix-femina, Boykinia occidentalis, Cardamine oligosperma, Clintonia andrewsiana, Disporum smithii, Dryopteris expansa, Equisetum telmateia, Galium triflorum, Lysichiton americanum, Maianthemum dilatatum, Marah oreganus, Mimulus dentatus, Satureja douglasii, Stachys ajugoides, Streptopus amplexifolius, Tolmiea menziesii, Trillium ovatum, Vancouveria hexandra,* and *Viola sempervirens* (Tables 7 and 8).

The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* Association

The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* association ranged from 18-299 m in elevation, averaging 136 m. Distance from the ocean averaged 3.6 km. Slopes averaged 50 percent, and MEI scores averaged 6.7. Species richness averaged 19.4 species (Table 6, Figures 7, 8, and 14).

Total vegetation cover averaged 93 percent, and total overstory cover averaged 71 percent. *Sequoia sempervirens* dominated the canopy, averaging 36 percent cover and 80 percent constancy. *Picea sitchensis* was common in coastal sites. *Pseudotsuga menziesii* and *Abies grandis* occurred sporadically. *Alnus rubra* dominated the subcanopy. *Acer macrophyllum, Lithocarpus densiflorus, Rhamnus purshiana, Sambucus racemosa*, and *Umbellularia californica* appeared occasionally in the subcanopy (Tables 7 and 8, Figure 9).

The 0-3 m tree layer was dominated by *Sequoia sempervirens* with 58 stems/ha, followed by, in decreasing order of abundance, *L. densiflorus*, *Alnus rubra*, and *P*.

Figure 14. *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* Association, Smith River, Jedediah Smith Redwoods State Park.

menziesii. The 3-10 m layer was dominated by *S. sempervirens* with 78 stems/ha, followed by *A. rubra, Abies grandis, Picea sitchensis*, and *L. densiflorus*. The >10m layer was dominated by *S. sempervirens* with 74 stems/ha, followed by *Alnus rubra, L. densiflorus, P. sitchensis, Pseudotsuga menziesii*, and *Abies grandis*. *Sequoia sempervirens* had the greatest total stems/ha (210), followed by *Alnus rubra, L. densiflorus, Picea sitchensis, Abies grandis*, and *Pseudotsuga menziesii* (Table 9). *Sequoia sempervirens* had the greatest basal area (87 m^2/ha) followed by, in decreasing order of abundance, *Picea sitchensis, Pseudotsuga menziesii*, and *A. grandis*. Total canopy basal area for this association averaged 107 m^2/ha (Table 10).

Rubus spectabilis dominated the moderately dense shrub layer, averaging 22 percent cover and 100 percent constancy. *Gaultheria shallon* was ubiquitous. Other common shrubs included *Acer circinatum, Corylus cornuta, Rubus parviflorus, R. ursinus*, and *Vaccinium ovatum* (Tables 7 and 8).

The herbaceous layer was diverse. *Polystichum munitum* dominated, averaging 24 percent cover and 100 percent constancy. *Oxalis oregana* occurred sporadically, but was generally abundant when it did occur. Other species included *Adiantum aleuticum, Asarum caudatum, Athyrium filix-femina, Blechnum spicant, Boykinia occidentalis, Carex deweyana, Cardamine oligosperma, Claytonia sibirica, Disporum smithii, Dryopteris expansa, Erechtites minima, Erechtites glomerata, Galium triflorum, Luzula comosa, Marah oreganus, Petasites frigidus, Phalarus arundinacea, Physocarpus capitatus,* *Polypodium glycyrrhiza, P. scouleri*, *Rubus discolor*, *Rubus ursinus, Rumex crispus, Stachys ajugoides, Tolmiea menziesii, Trillium ovatum*, and *Viola glabella* (Tables 7 and 8).

Discriminant Analysis

Discriminant analysis revealed that elevation, coastal proximity, and topographic position/aspect (MEI) were statistically significant ($p<.01$) in discriminating among floristic associations. Elevation and coastal proximity had the greatest influence on the first discriminant function (Table 11). This function explained 81.1% of the variation between groups. MEI had the greatest influence on the second discriminant function, which explained 14.2% of group variation (Table12). Together, the first two discriminant functions, influenced by elevation, distance to the ocean, and MEI, explained 95.3% of group variation. The physiographic factors influencing floristic associations, in decreasing order of importance, were elevation, coastal proximity, and aspect/topographic position (MEI).

Table 11. Standard Canonical Coefficients Used in Discriminant Analysis.

Variable	Variate 1	Variate 2	Variate 3	Variate 4
Elevation	-0.874009	0.717388	0.045912	-0.376631
Slope	0.189664	0.275203	0.477507	0.858742
Distance	-0.828487	-0.300679	-0.599034	0.465420
MEI	-0.376680	-1.100974	0.339726	0.143424

Table 12. Canonical Variate Analysis Section of Discriminant Analysis.

Function	Eigenvalue	Individual %	Total %	Canonical Corr.
1	1.026952	81.1	81.1	0.7118
2	0.180326	14.2	95.4	0.3909
3	0.049643	3.9	99.3	0.2175
4	0.009030	0.7	100.0	0.0946

DISCUSSION

Physiographic Relationships

Forest associations in the northern range of redwood were controlled primarily by moisture stress. Other redwood studies in the region (Whittaker 1960, Waring and Major 1964, Dyrness et al. 1972, Lenihan 1986, Matthews 1986) drew similar conclusions. The combination of elevation, coastal proximity, and aspect/topography created a moisture gradient extending from inland, high elevation, southwest facing upper slopes and ridges to coastal, low elevation, northeast facing lower slopes and valleys. Upper slopes and ridges at high elevations are generally xeric sites due to the shedding of water and soil material to lower slopes and elevations (Strahler and Strahler 1987, Kimmins 1997). South slopes are generally drier than north slopes in the region due to greater insolation on the former (Kimmins 1997). Inland locations in the region are generally drier due to the reduced presence of stratus and fog (National Weather Service 1998). Stratus and fog reduce evapotranspiration and fog drip adds supplemental moisture to the soil (Byers 1953, Roy 1966, Azvedo and Morgan 1974, Harris 1987). In addition, inland locations generally have greater temperature extremes, which may increase potential evapotranspiration (Zinke 1977).

Discriminant analysis revealed that elevation and coastal proximity were the most significant factors explaining the location of associations. Within these macro scale gradients, the combined microgradients of topographic position and aspect (in the form of the MEI) further accounted for the distribution of associations. The relationship between site factors and floristic associations is well correlated, but imperfect. The patchy mosaic of disturbance and recovery across the landscape, as well as other more subtle or unmeasured factors influencing species composition and stand structure, precluded perfect correlations.

Within this broad gradient, five associations separated themselves along a moisture continuum. Along this gradient, there was a general increase in conifer basal area and herbaceous biomass, and decrease in shrub biomass from xeric to mesic conditions. The associations, from xeric to mesic, were *Sequoia sempervirens-Pseudotsuga menziesii/ Rhododendron macrophyllum, Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum, Sequoia sempervirens/Polystichum munitum, Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum,* and *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis.* The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* association appeared to be controlled by a combination of abundant moisture and disturbance history.

Ecological Relationships

The *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum* Association

The SESE-PSME/RHMA association was frequently found in inland, high elevation (>250 m) upper slopes and ridges in SNF and coastal, high elevation upper slopes and ridges in

DNCRSP. Less frequent and persistent fog, minimal seepage water, and thin soils produced low basal areas of *Sequoia sempervirens* and *Pseudotsuga menziesii.* Open canopies allowed development of a dense tangle of shrub species such as *Vaccinium ovatum, Lithocarpus densiflorus,* and *Rhododendron macrophyllum*. *Pseudotsuga menziesii, L. densiflorus,* and *V. ovatum* are considered species with comparatively low minimum available moisture requirements (Waring and Major 1964), and this association was considered the most xeric in the study area. Sparse canopies and thick understories precluded development of a luxuriant herb layer, and, consequently, SESE-PSME/RHMA had the lowest herbaceous cover and species richness of all associations.

Veirs (1979) suggested *S. sempervirens* and *L. densiflorus* were components of the "climax" vegetation and would remain in the stand regardless of disturbance such as fire. The presence of *S. sempervirens* in all height classes suggested an all aged structure for redwood. Atzet and Wheeler (1984) suggested *L. densiflorus* will be the "climax" dominant in the absence of fire and other disturbances. They claimed the thick *L. densiflorus* cover will inhibit regeneration of other species and provide intense competition. Daubenmire (1975) claimed that, although *L. densiflorus* reproduces well, it poses no threat to the dominance of *S. sempervirens* due to the hardwood's small stature.

In the study area region, *P. menziesii* is a seral species that will disappear from stands without major disturbances such as intense fires (Daubenmire 1975, Veirs 1979, Eyre 1980). The low *P. menziesii* stem densities for the 0-3 m and 3-10 m height classes, and the high density of trees > 10 m, suggested that an even-aged cohort resulted from disturbance, and additional disturbances will be necessary for continued presence *of P. menziesii* in this association. Fire frequency was likely highest for this inland redwood type (Stuart 1987) relative to more mesic associations. Veirs (1979) suggested fires sufficient for abundant *P. menziesii* establishment in similar forests occur at 50 year intervals.

The *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum* Association

The SESE-TSHE/VAOV association was usually found in drier upper slopes and ridges at inland sites in JSRSP, and occasionally in drier sites in DNCRSP and SNF. It occurred in slightly more mesic sites than the SESE-PSME/RHMA association-- lower in elevation (<250 m), closer to the ocean (6-10 km), and in moister topographic positions and aspects. Consequently, *S. sempervirens* and *T. heterophylla* basal area increased while *P. menziesii* decreased, with a net increase in total canopy basal area. The denser canopy caused a reduction in small tree/large shrub cover, with *R. macrophyllum* and *L. densiflorus* decreasing while *V. ovatum* increased. Sparser shrub coverage resulted in greater herbaceous biomass. Species indicative of higher moisture, such as *Blechnum spicant* and *Polystichum munitum* (Waring and Major 1964) were present but low in cover. The greater diversity of mesic species indicated this association generally occupied wetter positions than the SESE-PSME/RHMA association along the moisture continuum.

The dominance of *T. heterophylla* in the SESE-TSHE/VAOV association was intriguing. The high density of *T. heterophylla* in the 0-3 m layer indicated extensive reproduction. *T. heterophylla* seedlings were especially abundant on downed logs. Combs (1984) noted a similar pattern of *T. heterophylla* regeneration in the Little Lost Man Creek Research Natural Area in Redwood National Park. He suggested that few seedlings would reach maturity because of vulnerability to fire and disease. Daubenmire (1975) noted extensive *T. heterophylla* in all size classes in JSRSP, but believed the species would decline without disturbance. Veirs (1979) suggested that light ground fires, unaffecting the canopy, will favor *T. heterophylla* regeneration. The high density of *T. heterophylla* and the complete absence of *P. menziesii* seedlings suggested a light fire regime, sufficient for *S. sempervirens* and *T. heterophylla* regeneration, but not for regeneration of *P. menziesii*. *Lithocarpus densiflorus*, though greatly reduced in density from the SESE-PSME/RHMA association, still maintained high stem densities in all height classes.

The *Sequoia sempervirens/Polystichum munitum* Association

The SESE/POMU association occurred throughout the study area, generally at mid slopes and elevations (<200 m), and at moderate distances (5-10 km) inland in JSRSP, RNP, and DNCRSP. *Sequoia sempervirens* greatly increased in basal area while all other canopy species decreased. There was an overall increase in basal area relative to SESE-

PSME/RHMA and SESE-TSHE/VAOV. *Sequoia sempervirens* attained it's greatest mean cover in this association. The small tree/tall shrub layer in general and *V. ovatum* in particular decreased dramatically in comparison to the two previous associations. *Polystichum munitum* dominated a dense and moderately species rich herbaceous layer. Canopy associates such as *Pseudotsuga menziesii* and *T. heterophylla* decreased in abundance, while herbaceous species such as *Oxalis oregana* and *Blechnum spicant* increased. SESE/POMU appeared more mesic than SESE-PSME/RHMA and SESE-TSHE/VAOV.

The SESE/POMU association showed high stem densities for *S. sempervirens* and *L. densiflorus* in the 0-3 m layer, the second highest density for *S. sempervirens* for all associations. *Abies grandis* and *T. heterophylla* were moderately dense, while *P. menziesii* was absent. *Sequoia sempervirens* dominated this association in all height classes. The moderate levels of *A. grandis, T. heterophylla*, and *L. densiflorus* reproduction may be indicative of the light fire regime in intermediate to mesic sites referred to by Veirs (1979). However, he noted that these species exhibited an all aged pattern and can reproduce regardless of fire.

The *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* Association

The SESE-TSHE/POMU association was generally found at lower slopes and elevations (<150m) 3-7 km inland in JSRSP. It was especially common in southwestern sections of the park heavily exposed to maritime influence. Persistent summer fog and abundant seepage water provided a mesic moisture regime. Consequently, *S. sempervirens* and *T. heterophylla* flourished. *Picea sitchensis* was occasional to common in coastal areas. SESE-TSHE/POMU had the highest *S. sempervirens* and total basal area. Dense canopies precluded the development of a rich shrub layer, and high cover of *Polystichum munitum* indicated deep shade and high moisture (Waring and Major 1964, Lenihan 1986). Additionally, increased dominance of mesic species like *Blechnum spicant* and *Rubus spectabilis* and decreased cover of more xeric species such *as L. densiflorus* and *V. ovatum* suggested mesic conditions (Waring and Major 1964).

The height structure of SESE-TSHE/POMU indicated *T. heterophylla* dominated the 0-3 m and 3-10 m layers. In the > 10 m layer, *S. sempervirens* and *T. heterophylla* shared dominance, while *Picea sitchensis* was occasional to common. *Tsuga heterophylla* showed similar size distribution to SESE-TSHE/VAOV. *Sequoia sempervirens* had fewer stems in the lower height classes relative to *T. heterophylla*, but the longevity and resilience of the former makes abundant individuals in the reproduction layers unnecessary to continued dominance of *S. sempervirens*.

The *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* Association

The SESE-TSHE/RUSP association was restricted to lower slopes and riparian areas of JSRSP, usually found at elevations less than 100 m and 4-9 km inland along Cedar Creek, Clarks Creek, Mill Creek, and other perennial drainages throughout interior JSRSP. Riparian conditions produced the wettest association encountered in the study area. Conifer basal area was greatly reduced compared to other associations. *Sequoia sempervirens* attained its lowest basal area, but still dominated conifer basal area. The uncommon *Thuja plicata* appeared occasionally. Riparian conditions allowed mesic woody species such as *Acer macrophyllum*, *A. circinatum*, *Corylus cornuta,* and *Rubus spectabilis* to thrive. In addition, mesic herbaceous species such as *Athyrium filix-femina, Blechnum spicant*, and *Oxalis oregana* (Waring and Major 1964) were abundant.

Height structure indicated high stem density for *T. heterophylla* in all height classes. *Sequoia sempervirens* showed its lowest density in all height classes in this association. *Lithocarpus densiflorus* showed increased stem density in this association after a steady decline along the moisture gradient. *Picea sitchensis* was common in coastal localities. As in the SESE-TSHE/VAOV and SESE-TSHE/POMU associations, *T. heterophylla* dominated the 0-3 m layer, indicating vigorous reproduction. The SESE-TSHE/RUSP association had the highest species richness of all associations, which, coupled with the presence of relatively uncommon species in the study area, such as *Thuja plicata*, makes this riparian forest association particularly significant ecologically.

The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* Association

The SESE-ALRU/RUSP association occurred in two general locations: riparian corridors along the Smith River, and coastal bluffs in DNCRSP. As a result, it appeared at relatively high elevations (>250 m) less than 1 km from the coast, or at low elevations (<75 m) along the Smith River 5-10 km inland. Conifer basal area remained low, with *S. sempervirens* dominating. *Picea sitchensis* was very common on coastal bluffs, and *Pseudotsuga menziesii* was common along the Smith River. *Alnus rubra* achieved high cover in the subcanopy. The mesic, high light environments of the Smith River floodplain and exposed coastal bluffs of DNCRSP provided favorable conditions for this shade intolerant hardwood (Hibbs et al. 1994, Harlow et al. 1996). Additionally, natural disturbance from Smith River flooding likely enhanced the competitive ability of *A. rubra*, which is more tolerant of flooding and poor drainage than its associates (Hibbs et al. 1994). Becking (1967) noted that moist, lower slope forests within the Redwood-Oxalis alliance were prone to slipouts, and these disturbed sites were quickly colonized by *A. rubra*. In addition, self-perpetuating *A. rubra* stands occur throughout the region (Sawyer and Keeler-Wolf 1995). Tolerance of salt spray and resistance to windthrow (Hibbs et al. 1994) allowed *A. rubra* to thrive along the coastal bluffs of DNCRSP. Periodic disturbances likely benefited the seral *Pseudotsuga menziesii*.

The height structure of this association indicated abundant *S. sempervirens* stems in all height classes, with the highest total stem density of all associations. *Alnus rubra* showed high stem densities in the 3-10 and >10 m height classes, but minimal density in the 0-3 m class, indicating many stands in SESE-ALRU/RUSP may be recovering from disturbance. The SESE-ALRU/RUSP association had the second highest species richness of all associations. The riparian conditions as well as possible disturbance likely contributed to the high species richness in this association.

Relationships to Previous Classifications

The six associations described in the current study were all part of the *Pseudotsuga-Sequoia* forests described by Küchler (1977). Additionally, the SESE-TSHE/POMU, SESE-TSHE/RUSP, and SESE-ALRU/RUSP associations contained elements of Küchler's (1977) *Abies-Picea* forest. All six associations corresponded to the Society of American Foresters (Eyre 1980) Redwood forest type, though the SESE-PSME/RHMA and SESE-TSHE/VAOV associations contained elements of the Pacific Douglas-fir forest type, while SESE-TSHE/POMU related to the Western hemlock forest type. In addition, the six associations described in the current study can be tentatively included in the *Picea sitchensis* Zone described by Franklin and Dyrness (1973).

The SESE-PSME/RHMA association might be considered an extension of the *Pseudotsuga*-hardwood forests described by Sawyer et al. (1977). It was similar in composition to forests they described dominated by *Pseudotsuga menziesii*, with a continuous lower canopy of *Lithocarpus densiflorus*. SESE-PSME/RHMA closely resembled the midslope stands, with thick understories of *Lithocarpus densiflorus, Vaccinium ovatum,* and *Rhododendron macrophyllum,* encountered by Dyrness et al. (1972) in Wheeler Creek Research Natural Area. Indeed, several stands sampled in the current study were located in this Natural Area. The Tanoak-coast redwood association, described by Atzet and Wheeler (1984) for southwestern Oregon, resembled the SESE-PSME/RHMA association described in the current study. The SESE-PSME/RHMA association roughly related to the *Sequoia sempervirens-Pseudotsuga menziesii/ Vaccinium ovatum* association described by Matthews (1986) for Humboldt Redwoods State Park. The main difference was the absence of *Rhododendron macrophyllum* in Matthews' association. Additionally, the SESE-PSME/RHMA association contained elements of the *Sequoia sempervirens/Arbutus menziesii* association described by Lenihan (1986), the primary difference being the absence of *Arbutus menziesii* in the former. SESE-PSME/RHMA contained many similarities to Becking's (1967) Redwood-swordfern alliance.

The SESE-TSHE/VAOV association was unique compared to other redwood types described in the literature due to the importance of *Tsuga heterophylla*. While other redwood classifications have noted the presence of *T. heterophylla* (Dyrness et al. 1972, Atzet and

Wheeler 1984, Lenihan 1986), none have shown such dominance by this mesic conifer. The *Sequoia sempervirens/Berberis nervosa* association described by Lenihan (1986) contained many elements of SESE-TSHE/VAOV. Sawyer et al. (1977) noted a *Tsuga* phase of the *Pseudotsuga*-hardwood forests similar in composition to this association. SESE-TSHE/VAOV can be tentatively assigned to the Redwood-swordfern alliance proposed by Becking (1967).

The SESE/POMU association contained elements of the *Sequoia sempervirens/Blechnum spicant* association described by Lenihan (1986), though Lenihan's association appeared wetter. The dominance of *Sequoia sempervirens*, the sparse shrub layer, and the well-developed herb layer related SESE/POMU to Becking's (1967) Redwood-oxalis alliance.

The SESE-TSHE/POMU association, like SESE-TSHE/VAOV, appeared unlike any previously described redwood types. It was similar in many respects to the mesic *Tsuga/Polystichum* association described by Franklin and Dyrness (1973) for Oregon Coast Range forests in the *Tsuga heterophylla* Zone. Additionally, it contained elements of the *Tsuga-Picea/Oplopanax horridum/Athyrium filix-femina* association of *Picea sitchensis* Zone forests described by Franklin and Dyrness (1973). It related tangentially to Lenihan's (1986) *Sequoia sempervirens/Blechnum spicant* association, though the dominance of *T. heterophylla* in SESE-TSHE/POMU was much greater than in Lenihan's association.

The SESE-TSHE/RUSP association appeared much wetter than any redwood association previously described. It shared many of the same riparian components, such as high cover of herbaceous and hardwood species, described by Dyrness et al. (1972) for lower slopes in the

Wheeler Creek Research Natural Area in southwestern Oregon. SESE-TSHE/RUSP appeared similar in many respects to the *Tsuga heterophylla/Acer circinatum/Polystichum munitum-Oxalis oregana* association described by Franklin and Dyrness (1973) for alluvial terrace vegetation in the *Tsuga heterophylla* Zone of Oregon. The absence of *Sequoia sempervirens* in *Tsuga heterophylla* Zone forests makes comparison difficult, however.

The SESE-ALRU/RUSP association was similar to coastal sections of the Wildcat Hills transect described by Zinke (1977). He described a forest of *Picea sitchensis, Abies grandis,* and *Pseudotsuga menziesii,* with *Alnus rubra* in disturbed locations. The red alder series described in Sawyer and Keeler-Wolf (1995) was similar in some respects to SESE-ALRU/RUSP.

Though the associations described in this study were all classified in the *Sequoia sempervirens* series, one might argue for placement into other series, such as *Pseudotsuga menziesii, Tsuga heterophylla,* and *Alnus rubra.* However, Sawyer and Keeler-Wolf (1995) define the *S. sempervirens* series as having "redwood the sole, dominant, or important tree in canopy". The "important" distinction is not part of the definition of *Pseudotsuga menziesii, Tsuga heterophylla,* or *Alnus rubra* series forests. The huge *S. sempervirens* basal area in all associations underscores both it's importance and ecological dominance, and therefore all associations were placed in the *S. sempervirens* series.

Conclusions

The northern range of redwood was divided into six associations, all in the *Sequoia sempervirens* series. They were controlled primarily by a moisture gradient extending from inland, high elevation, upper slopes and ridges on xeric aspects to coastal, low elevation, lower slopes and riparian zones on mesic aspects. Elevation and coastal proximity are the most important factors differentiating the vegetation types. The associations, from xeric to mesic, are *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum, Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum, Sequoia sempervirens/Polystichum munitum, Sequoia sempervirens-Tsuga heterophylla/ Polystichum munitum,* and *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis.* The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* association resulted from mesic conditions and disturbance. Generally, conifer basal area, herbaceous biomass, and species richness increased and shrub biomass decreased from xeric to mesic sites. The outstanding feature of the northern range of redwood, compared to previous classifications, was the abundance of *Tsuga heterophylla*.

REFERENCES CITED

Aalto, K.R. and G.D. Harper. 1989. Geologic evolution of the northernmost coast ranges and western Klamath mountains, California. American Geophysical Union. Washington, D.C.

Atzet, T. and D.L. Wheeler. 1984. Preliminary plant associations of the Siskiyou Mountain Province. USDA Forest Service Pacific Northwest Region. 315 p.

Azvedo, J. and D.L. Morgan. 1974. Fog precipitation in coastal California forests. Ecology 55:1135-1141.

Bachman, S.B., M.B. Underwood, and J.S. Menack. 1984. Cenozoic evolution of coastal northern California. Pp. 55-66 *in*: J.K. Crouch and S.B. Bachman (eds.), Tectonics and sedimentation along the California margin: Pacific Section, Society of Economic Paleontologists and Mineralogists. 188 pp.

Becking, R.W. 1967. The ecology of the coastal redwood forest and the impact of the 1964 floods upon redwood vegetation. Final Report. NSF Grant GB No. 3468. 91 p.

__________1971. The ecology of the coastal redwood forest of northern California and the impact of the 1964 flood upon redwood vegetation. Final Report. NSF Grant GB No. 6310. 158 p.

Borchert, M., D. Segotta, and M.D. Purser. 1988. Coast redwood ecological types of southern Monterey county, California. USDA Forest Service research paper PSW-107. Pacific Southwest Forest and Range Experiment Station. Berkeley, California. 27 p.

Byers, H.R. 1953. Coast redwood and fog drip. Ecology 34:192-193.

Combs, W.E. 1984. Stand structure and composition of the Little Lost Man Creek Research Natural Area, Redwood National Park. M.S. thesis, Humboldt State University. Arcata, California. 93 p.

Daubenmire, R.W. 1975. The community status of the coastal redwood, *Sequoia sempervirens*: A report prepared for the National Park Service. Arcata, California. 17 p.

DeLapp, J.A., B.F. Smith, and W.R. Powell. 1978. Soil-vegetation map and legend- N1/2 of Klamath quadrangle (9D-1,2). California Cooperative Soil-Vegetation Survey. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. Berkeley, California. 11p.

Dyrness, C.T., J.F. Franklin, and C. Maser. 1972. Wheeler Creek Research Natural Area, federal research natural areas in Oregon and Washington: A guidebook for scientists and educators. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. Supplement No.1. 16 p.

ECOMAP. 1993. National hierarchical framework of ecological units. Unpublished document. USDA Forest Service, Washington D.C.

Eyre, F.H. (ed). 1980. Forest cover types of the United States and Canada. Society of American Foresters. Washington, D.C. 148 p.

Fox, Lawrence III. 1989. A classification, map and volume estimate for the coast redwood forest in California. Final report. Interagency agreement number 8CA52849. The Forest and Rangeland Resources Assessment Program. California Department of Forestry and Fire Protection. Sacramento, California. 37 p.

Franklin, J.F., and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 417 p.

Freeman, G.J. 1971. Summer fog drip in the coastal redwood forest. M.S. thesis, Humboldt State University, Arcata, California. 100 p.

Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press. New York. 298 p.

Gauch, H.G. Jr., R.H. Whittaker and T.R. Wentworth. 1977. A comparative study of reciprocal averaging and other ordination techniques. Journal of Ecology 65:157-174.

Harlow, W.M., E.S. Harrar, J.W. Hardin, and F.M. White. 1996. Textbook of dendrology. McGraw-Hill, Inc., New York. 534 p.

Harris, S.A. 1987. Relationship of convection fog to characteristics of the vegetation of Redwood National Park. M.S. thesis, Humboldt State University, Arcata, California. 60 p.

Hibbs, D.E., D.S. DeBell, and R.F. Tarrant. 1994. The biology and management of red alder. Oregon State University Press, Corvallis, Oregon. 256 p.

Hickman, J.C.(ed). 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, California. 1400p.

Hill, M.O. 1979. TWINSPAN: A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University. Ithaca, New York. 90p.

Hintze, J.L. 1998. NCSS 2000. NCSS, Kaysville, Utah. 91 p.

Kimmins, J.P. 1997. Forest ecology: a foundation for sustainable management. Prentice Hall, Upper Saddle River, New Jersey. 596 p.

Klecka, W.R. 1980. Discriminant analysis. Sage Publications, London, England. 71 p.

Küchler, A.W. 1977. The map of the natural vegetation of California. Pp. 909-938 *in* M.G. Barbour and J. Major (eds.), Terrestrial vegetation of California. John Wiley and Sons, New York. 1002 p.

Lenihan, J.M. 1986. The forest associations of the Little Lost Man Creek Research Natural Area, Redwood National Park, CA. M.S. thesis, Humboldt State University, Arcata, California. 85 p.

Matthews, S.C. 1986. Old-growth forest associations of the Bull Creek watershed Humboldt Redwoods State Park, California. M.S. thesis, Humboldt State University, Arcata, California. 93 p.

McBride, J., and D. Jacobs. 1977. The ecology of redwood (*Sequoia sempervirens* (D. Don) Endl.) and the impact of man's use of the redwood forest as a site for recreational activities. Report prepared for the U.S. National Park Service. Berkeley, California. 39 p.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 p.

National Weather Service. 1998. The climate of Humboldt and Del Norte Counties. Unpublished report. Eurkea, California. 16 p. (on file at the National Weather Service office, Eureka, California).

Redwood National and State Parks. 1998. Draft General Management Plan. Redwood National and State Parks, Crescent City, California. 458 p.

Roy, D.F. 1966. Silvicultural characteristics of redwood. USDA Forest Service research paper PSW-28. PSW Forest and Range Experiment Station. Berkeley, California. 20 p.

Sawyer, J.O., and T. Keeler-Wolf. 1995. A manual of California vegetation. California Native Plant Society, Sacramento, California. 470 p.

Sawyer, J.O. and D.A. Thornburgh. 1974. Subalpine and montane forests on granodiorite in the central Klamath mountains of California. Report to PSW Forest and Range Experiment Station and Humboldt State University, Arcata, California. 45 p.

Sawyer, J.O., D.A. Thornburgh, and J.R. Griffin. 1977. Mixed evergreen forest. Pp. 359- 381 *in:* M.G. Barbour and J. Major (eds.), Terrestrial vegetation of California. John Wiley and Sons, New York. 1002 p.

Smith, B.F., J.A. Delapp, and W.R. Powell. 1977. Soil-vegetation map and legend- S1/2 Crescent City quadrangle (9A-3,4). California Cooperative Soil-Vegetation Survey. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. Berkeley, California. 10p.

Strahler A.N., and A.H. Strahler. 1987. Modern physical geography. John Wiley and Sons, New York. 544 p.

Stuart, J.D. 1987. Fire history of an old-growth forest of *Sequoia sempervirens* (Taxodiaceae) forest in Humboldt Redwoods State Park, California. Madroño 34: 128-141.

Stuart, J.D., T. Worley, and A.C. Buell. 1996. Plant associations of Castle Crags State Park, Shasta County, California. Madroño 43: 273-291.

Veirs, S.D., Jr. 1979. The role of fire in northern coast redwood forest dynamics. Proceedings from the Second Conference on Scientific Research in the National Parks, San Francisco, California.

Waring, R.H. and J. Major. 1964. Some vegetation of the California coastal region in relation to gradients of moisture, nutrients, light, and temperature. Ecological Monographs 34:167-215.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279-338.

Zinke, P.J. 1977. The redwood forest and associated north coast forests. Pp. 679-698 *in*: M.G. Barbour and J. Major (eds.), Terrestrial vegetation of California. John Wiley and Sons Publishers. New York. 1002 p.

APPENDIX A. Vascular Plant Species Found in Study Area. Nomenclature Follows *The Jepson Manual* (Hickman 1993).

ACERACEAE

Acer circinatum Pursh
Acer macrophyllum Pursh

ANACARDIACEAE

Rhus trilobata Torrey & A. Gray
Toxicodendron diversilobum (Torrey & A. Gray) E. Greene

APIACEAE

Angelica arguta Nutt.
Oenanthe sarmentosa J.S. Presl
Osmorhiza chilensis Hook. & Arn.
Sanicula crassicaulis DC.

AQUIFOLIACEAE

Ilex aquifolium L.

ARACEAE

Lysichiton americanum Hulten & St. John

ARISTOLOCHIACEAE

Asarum caudatum Lindley

ASTERACEAE

Achillea millefolium L.
Adenocaulon bicolor Hook.
Anaphalis margaritacea (L.) Benth. & Hook.
Artemisia douglasiana Besser
Baccharis pilularis DC.
Erechtites glomerata (Poiret) DC.
Erechtites minima (Poiret) DC.
Erigeron philadelphicus L.
Gnaphalium purpureum L.
Hypochaeris radicata L.
Madia madioides (Nutt.) E. Greene
Microseris laciniata (Hook.) Schultz-Bip. ssp. *leptosepala* (Nutt.) Chambers
Petasites frigidus (L.) Fries var. *palmatus* (Aiton) Cronq.

APPENDIX A. Vascular Plant Species Found in Study Area (Continued).

BERBERIDACEAE

Achlys californica I. Fukuda & H.G. Baker
Berberis nervosa Pursh
Vancouveria hexandra (Hook.) Morren & Decne.
Vancouveria planipetala Calloni

BETULACEAE

Alnus rubra Bong.
Corylus cornuta Marsh. var. *californica* (A. DC.) W. Sharp

BLECHNACEAE

Blechnum spicant (L.) Smith

BRASSICACEAE

Cardamine californica (Torrey & A. Gray) E. Greene var. *sinuata* (E. Greene) O. Schulz
Cardamine oligosperma Torrey & A. Gray

CAPRIFOLIACEAE

Lonicera involucrata (Richardson) Banks var. *ledebourii* (Eschsch.) Jepson
Lonicera hispidula Douglas var. *vacillans* A. Gray
Sambucus racemosa L. var. *racemosa*
Symphoricarpos albus (L.) S.F. Blake var. *laevigatus* (Fern.) S.F. Blake

CARYOPHYLLACEAE

Cerastium glomeratum Thuill.
Dianthus barbatus L. ssp. *barbatus*
Silene gallica L.
Stellaria media (L.) Villars

CELASTRACEAE

Euonymus occidentalis Torrey var. *occidentalis*

CORNACEAE

Cornus nuttallii Audubon

CUCURBITACEAE

Marah oreganus (Torrey & A. Gray) Howell

APPENDIX A. Vascular Plant Species Found in Study Area (Continued).

CUPRESSACEAE
Cupressus lawsoniana A. Murray
Thuja plicata D. Don

CYPERACEAE
Carex aquatilis Wahlenb. var. *aquatilis*
Carex deweyana Schwein ssp. *leptopoda* (Mackenzie) Calder & R. Taylor
Carex hendersonii L. Bailey
Cyperus niger Ruiz Lopez & Pavon
Carex obnupta L. Bailey

DENNSTAEDTIACEAE
Pteridium aquilinum (L.) Kuhn var. *pubescens* L. Underw.

DRYOPTERIDACEAE
Athyrium filix-femina (L.) Roth var. *cyclosorum* Rupr.
Cystopteris fragilis (L.) Bernh.
Dryopteris expansa (C. Presl) C.R. Fraser-Jenkins & Jermy
Polystichum munitum (Kaulf.) C. Presl

EQUISETACEAE
Equisetum arvense L.
Equisetum hyemale L. ssp. *affine* (Engelm.) Calder & R.H. Taylor
Equisetum telmateia Ehrh. ssp. *braunii* (Milde) R.L. Hauke

ERICACEAE
Chimaphila menziesii (D. Don) Sprengel
Gaultheria shallon Pursh
Menziesia ferruginea Smith
Pityopus californicus (Eastw.) H.Copel.
Pleuricospora fimbriolata A. Gray
Pyrola picta Smith
Rhododendron macrophyllum D. Don
Rhododendron occidentale (Torrey & A. Gray). A. Gray
Vaccinium ovatum Pursh

Vaccinium parvifolium Smith

APPENDIX A. Vascular Plant Species Found in Study Area (Continued).

FABACEAE
Cytisus scoparius (L.) Link
Lathyrus vestitus Nutt.
Trifolium pratense L.
Lithocarpus densiflorus (Hook & Am.) Rehder

GROSSULARIACEAE
Ribes bracteosum Douglas
Ribes menziesii Pursh
Ribes sanguineum Pursh

IRIDACEAE
Iris douglasiana Herbert

JUNCACEAE
Juncus effusus L. var. *pacificus* Fern. & Wieg.
Luzula comosa E. Meyer

LAMIACEAE
Prunella vulgaris L.
Satureja douglasii (Benth.) Briq
Stachys ajugoides Benth. var. *ajugoides*
Stachys ajugoides Benth. var. *rigida* Jepson & Hoover

LAURACEAE
Umbellularia californica (Hook. & Am.) Nutt.

LILIACEAE
Clintonia andrewsiana Torrey
Disporum hookeri (Torrey) Nicholson
Disporum smithii (Hook.) Piper
Lilium columbianum Baker
Maianthemum dilatatum (Alph. Wood) Nelson & J.F. Macbr.

Smilacina racemosa (L.) Link
Streptopus amplexifolius (L.) DC var. *americanus* Schultes
Trillium ovatum Pursh spp. *ovatum*
Triteleia bridgesii (S. Watson) E. Greene

MYRICACEAE
Myrica californica Cham.
APPENDIX A. Vascular Plant Species Found in Study Area (Continued).

OLEACEAE
Fraxinus latifolia Benth.

ORCHIDACEAE
Corallorhiza maculata Raf.
Corallorhiza mertensiana Bong.
Cypripedium californicum A. Gray
Goodyera oblongifolia Raf.

ORCHIDACEAE
Listera caurina Piper
Listera cordata (L.) R.Br.

OROBANCHACEAE
Boschniakia hookeri Walp.

OXALIDACEAE
Oxalis oregana Nutt.

PHILADELPHACEAE
Whipplea modesta Torrey

PINACEAE
Abies grandis (Douglas) Lindley
Picea sitchensis (Bong.) Carriere
Pseudotsuga menziesii (Mirbel) Franco var. *menziesii*
Tsuga heterophylla (Raf.) Sarg.

PLANTAGINACEAE
Plantago lanceolata L.

POACEAE

Agrostis hallii Vasey.
Anthoxanthum odoratum L.
Bromus diandrus Roth
Bromus hordeaceus L.
Bromus vulgaris (Hook.) Shear
Calamagrostis canadensis (Michaux) Beauv.
Cynosurus echinatus L.
Elymus glaucus Buckley ssp. *glaucus*

APPENDIX A. Vascular Plant Species Found in Study Area (Continued).

POACEAE

Festuca arundinacea Schreber
Festuca occidentalis Hook.
Festuca subulata Trin.
Glyceria elata (Nash) M.E. Jones
Hierochloe occidentalis Buckley
Holcus lanatus L.
Melica subulata (Gris.) Scribner
Panicum acuminatum Sw. var. *acuminatum*
Phalaris arundinacea L.
Pleuropogon refractus (A. Gray) Benth.
Poa trivialis L.
Trisetum cernuum Trin.

POLEMONIACEAE

Collomia heterophylla Hook.

POLYGONACEAE

Rumex acetosella L.
Rumex crispus L.

POLYPODIACEAE

Polypodium calirhiza S. Whitmore & A.R. Smith
Polypodium glycyrrhiza D. Eaton
Polypodium scouleri Hook. & Grev.

PORTULACACEAE

Claytonia sibirica L.
Montia parvifolia (DC.) E. Greene

PRIMULACEAE
Trientalis latifolia Hook.

PTERIDACEAE
Adiantum aleuticum (Rupr.) C.A. Paris
Pentagramma triangularis (Kaulf.) G. Yatskievych, M.D. Windham & E. Wollenweber

APPENDIX A. Vascular Plant Species Found in Study Area (Continued).

RANUNCULACEAE
Actaea rubra (Aiton) Willd.
Aquilegia formosa Fischer
Ranunculus repens L.

RHAMNACEAE
Rhamnus purshiana DC.

ROSACEAE
Amelanchier alnifolia (Nutt.) Nutt. var. *semiintegrifolia* (Hook.) C. Hitchc
Amelanchier utahensis Koehne
Aruncus dioicus (Walter) Fern. var. *pubescens* (Rydb.) Fern.
Cotoneaster pannosa Franchet
Holodiscus discolor (Pursh) Maxim.
Oemleria cerasiformis (Hook. & Arn.) J.W. Landon
Physocarpus capitatus (Pursh) Kuntze
Rosa gymnocarpa Nutt.
Rosa pisocarpa A. Gray

ROSACEAE
Rubus discolor Weihe & Nees
Rubus parviflorus Nutt.
Rubus spectabilis Pursh
Rubus ursinus Cham. & Schldl.

RUBIACEAE
Galium triflorum Michaux

SALICACEAE
Salix lucida Muhlenb. ssp. *lasiandra* (Benth.) E. Murray

SAXIFRAGACEAE
Boykinia occidentalis Torrey & A. Gray
Tolmiea menziesii (Pursh) Torrey & A. Gray

SCROPHULARIACEAE
Digitalis purpurea L.
Mimulus dentatus Benth.
Veronica americana (Raf.) Benth.

APPENDIX A. Vascular Plant Species Found in Study Area (Continued).

TAXODIACEAE
Sequoia sempervirens (D. Don) Endl.

URTICACEAE
Urtica dioica L. ssp. *gracilis* (Aiton) Selander

VIOLACEAE
Viola glabella Nutt.
Viola sempervirens E. Greene

APPENDIX B. Field Key to Old-Growth Forest Associations in the Northern Range of Redwood.

1. *Vaccinium ovatum* cover greater than 40%; *Polystichum munitum* cover less than 20%. *Pseudotsuga menziesii* common..2

2. *Tsuga heterophylla* cover greater than 10%. *Lithocarpus densiflorus* and *Rhododendron macrophyllum* common but cover less than 25%.

Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum Association

2. *Tsuga heterophylla* cover less than 10%. *Lithocarpus densiflorus* and *Rhododendron macrophyllum* very dense in the small tree/large shrub layer, with cover greater than 25%.

Sequoia sempervirens-Pseudotsuga menziesii/ Rhododendron macrophyllum Association

1. *Vaccinium ovatum* cover less than 40%; *Polystichum munitum* cover greater than 20%. *Pseudotsuga menziesii* uncommon..3

3. *Alnus rubra* subcanopy coverage greater than 10%. *Tsuga heterophylla* absent.

Sequoia sempervirens-Alnus rubra/Rubus spectabilis Association

3. *Alnus rubra* subcanopy coverage less than 10%. *Tsuga heterophylla* present..4

4. *Acer circinatum* cover greater than 10%. *Acer macrophyllum* cover greater than 5%. *Polystichum munitum* cover less than 40%. *Rubus spectabilis* cover greater than 10%.

Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis Association

4. *Acer circinatum* cover less than 10%. *Acer macrophyllum* cover less than 5%. *Polystichum munitum* cover greater than 40%. *Rubus spectabilis* cover less than 10%...5

5. *Lithocarpus densiflorus* cover greater than 5%. *Blechnum spicant* cover less than 5%. *Tsuga heterophylla* cover less than 30%.

Sequoia sempervirens/Polystichum munitum Association

APPENDIX B. Field Key to Old-Growth Forest Associations in the Northern Range of Redwood (Continued).

5. *Lithocarpus densiflorus* cover less than 5%. *Blechnum spicant* cover greater than 5%. *Tsuga heterophylla* cover greater than 30%.

Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum Association